

Q1
Ip91
C.2

Ve

Iowa State Journal of Research

Volume 54, No. 3

ISSN 0092-6345

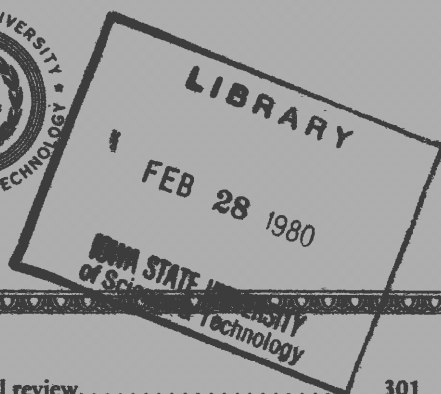
February, 1980

ISJRA6

54(3)

299-415

1980



THOMASSON, J.R. Paleocrostopology: a historical review.	301
POHL, R.W. <i>Eragrostis bondurensis</i> , a new grass species from Central America (Gramineae: Chloridoideae: Eragrosteae)	319
HEIN, M.K. Flora of Adak Island, Alaska: lichens, liverworts, mosses	323
NIELSEN, D.C. and R.H. SHAW. Irrigation potential on Iowa soils of high water- holding capacity	329
PEASE, D.G. and D.F. ANDERSON. Relationships of previous sport participa- tion, age, and sex with expressed attitudes toward sport team participation . . .	339
ONUKOGU, F.A., W.D. GUTHRIE, W.H. AWADALLAH, and J.C. ROBBINS. Hatchability of eggs and mating success of European corn borer cultures reared continuously on a meridic diet	347
GUTHRIE, W.D., F.A. ONUKOGU, W.H. AWADALLAH, and J.C. ROBBINS. Behavior and survival of cultures of European corn borers reared on a meridic diet in dishes	357
EDWARDS, C.R., E.C. BERRY, and T.A. BRINDLEY. Effect of insecticide applications on insect predators of the European corn borer in central Iowa . .	361
RODRIGUEZ de CIANZIO, S. and W.R. FEHR. Genetic control of iron defi- ciency chlorosis in soybeans	367
BURRIS, J.S. Maintenance of soybean seed quality in storage as influenced by moisture, temperature, and genotype	377
JARVIS, J.L. Resistance in sunflowers to sunflower moth	391
SZABO, J.P. Quaternary stratigraphy of the lower part of Pioneer Creek Basin, Cedar and Jones Counties, Iowa	401

**IOWA STATE
JOURNAL OF RESEARCH**

Published under the auspices of the Graduate College of Iowa State University
August, November, February, and May

EDITOR **DUANE ISELY**
ASSOCIATE EDITOR **KENNETH G. MADISON**
BUSINESS MANAGER **MERRITT E. BAILLY**

Administrative Board

W. J. Ulmer, Chairman
M. E. Bailey, I.S.U. Press
W. H. Schmitt, Information Service
W. A. Russell, College of Science and Humanities
J. E. Galejs, I.S.U. Library
W. R. Madden, Office of Business and Finance
J. P. Mahlerede, Agriculture and Home Economics Experiment Station
G. K. Seisoy, College of Engineering
Duane Iseely, Editor

Editorial Board

Floyd Miner, University of Arkansas, Associate Editor for Entomology
Clive Jorgensen, Brigham Young University, Associate Editor for Zoology
Paul Barcus, Iowa State University, Consultant for Engineering

Secretary

Christine McDaniel

Manuscripts should be submitted to the Editor, Duane Iseely, 343 Bessey Hall, Iowa State University, Ames, Iowa 50011.

All matters pertaining to subscriptions, remittances, etc., should be addressed to the Iowa State University Press, South State Avenue, Ames, Iowa 50010. Subscription rates are as follows: Annual, \$16.00 (Canada, \$17.00; other foreign countries, \$20.00); Single copies starting with Volume 34 are \$6.00 each plus postage. Prior issues are \$4.50 each, plus postage.

Most back issues of the IOWA STATE JOURNAL OF RESEARCH are available. Prices will be furnished by the Iowa State University Press upon request. Because of limited stocks, payment is required prior to shipment.

Second-class postage paid at Ames, Iowa 50011.

IOWA STATE JOURNAL OF RESEARCH
TABLE OF CONTENTS
Volume 54
(August, 1979–May, 1980)

No. 1, August, 1979

THOBURN, W.C. Tension in the interface between two liquids.	1
THOBURN, W.C. Tension in the interface between a liquid and a solid. .	9
SIVAKUMAR, M.V.K. and R.H. SHAW. Stomatal conductance and leaf-water potential of soybeans under moisture stress	17
WHEELER, A.G. A comparison of the plant-bug fauna of the Ithaca, New York area in 1910-1919 with that in 1978	29
GEORGE, J.R. and W.E. KNOOP. A strip-tillage interseeder for simu- lated pasture renovation in small experimental plots.	37
JAY, F.B. and R.J. MUNCY. Toxicity to channel catfish of wastewater from an Iowa coal beneficiation plant.	45
KLAIBER, F.W. and K.H. PONDER. Summary of energy survey of Iowa industry	51
HADWIGER, D.F. and M. MILLER. Regulation of pesticides by the State of Iowa.	65
BARKMAN, L.L. and H.A. JAMES. A population study of monogene- tic trematodes from the killifish, <i>Fundulus heteroclitus</i> (Linnaeus) in Connecticut.	77
BOLES, D.E. The impact of corporate agricultural land ownership on rural and local government: some preliminary observations	83
Author-title list of theses and dissertations, Iowa State University (Summer, 1978–Spring, 1979).	117

* * * * *

No. 2, November, 1979

TECHNOLOGY AND HUMAN VALUES: STUDIES IN THE
INTERACTION OF TECHNOLOGY, SOCIETY
AND THE HUMANITIES
Symposium
April 20-22, 1977

FERKISS, V. Foreward	161
KRANZBERG, M. Technology the civilizer.	163
MULTHAUF, R.P. What the chemists found in Pandora's box: A brief history of the chlorinated hydrocarbons	175
GARSIDE, P.L. Innovation and social values: The example of France, Britain and the United States in the nineteenth century	185
HUANG, S. Changing Taiwanese peasants' concept of time: Its impact on agricultural production	191
PATTEN, S.E. The primacy of structure over event: The case of the Tallensi of Northern Ghana.	201

SOLOMON, T.J. "The supreme consideration is man": Gandhi's critique of modern technology 209

SCHMIDT, S.W. Technology, culture and development in Latin America. 217

ROBINSON, S.K. Pouring new technology into old cottages 225

CAWS, P. Toward a philosophy of technology 229

ROBINSON, W.S. Technology and values: Some preliminary clarifications 241

AMELINCKX, F.C. Man, machines and moral order: Technology and values in French romanticism 249

FOLSOM, J.K. Magic and technology as opposing values in science fiction 257

BENSON, D. Zen and the art of motorcycle maintenance: Technology re-valued 267

SCHLEGEL, R. Technology and its values. 275

HOLLINGER, R. On some moral objections to technology. 283

FERKISS, V. Technology and values: From dialectic toward synthesis 291

* * * * *

No. 3, February, 1980

THOMASSON, J.R. Paleoagrostology: a historical review. 301

POHL, R.W. *Eragrostis hondurensis*, a new grass species from Central America (Gramineae: Chloridoideae: Eragrosteae) 319

HEIN, M.K. Flora of Adak Island, Alaska: lichens, liverworts, mosses. 323

NIELSEN, D.C. and R.H. SHAW. Irrigation potential on Iowa soils of high water-holding capacity. 329

PEASE, D.G. and D.F. ANDERSON. Relationships of previous sport participation, age, and sex with expressed attitudes toward sport team participation 339

ONUKOGU, F.A., W.D. GUTHRIE, W.H. AWADALLAH, and J.C. ROBBINS. Hatchability of eggs and mating success of European corn borer cultures reared continuously on a meridic diet 347

GUTHRIE, W.D., F.A. ONUKOGU, W.H. AWADALLAH, and J.C. ROBBINS. Behavior and survival of cultures of European corn borers reared on a meridic diet in dishes 357

EDWARDS, C.R., E.C. BERRY, and T.A. BRINDLEY. Effect of insecticide applications on insect predators of the European corn borer in central Iowa. 361

RODRIGUEZ de CIANZIO, S. and W.R. FEHR. Genetic control of iron deficiency chlorosis in soybeans 367

BURRIS, J.S. Maintenance of soybean seed quality in storage as influenced by moisture, temperature, and genotype 377

JARVIS, J.L. Resistance in sunflowers to sunflower moth. 391

SZABO, J.P. Quaternary stratigraphy of the lower part of Pioneer Creek Basin, Cedar and Jones Counties, Iowa 401

No. 4, May, 1980

ASPECTS IN SHAKESPEAREAN SCHOLARSHIP II
PAPERS PRESENTED AT
"MUCH ADO ABOUT SHAKESPEARE"
Symposium, 1979

GALYON, L.R. Introduction	419
FORKER, C.R. All the world's a stage: Multiple perspectives in Arden	421
PERRET, M. Of sows' ears and silk purses: Transformation images in <i>The Taming of the Shrew</i>	431
PALMER, B.D. "The eagles are gone": Soliloquies in the tragi-comedies	441
PARTEE, M.H. The function of Cordelia	449
TYSON, E.S. Shakespeare's <i>Macbeth</i> and Dante's <i>Inferno</i> : A comparison of the images of hell, damnation, and corruption.	461
STUGRIN, M. "But I must also feel it as a man": Pathos and knowledge in Shakespearean tragedy.	469
FORD, P.J. Bloody spectacle in Shakespeare's Roman plays: The politics and aesthetics of violence.	481
CANDIDO, J. Katherine of Aragon and female greatness: Shakespeare's debt to dramatic tradition.	491

Vol. 54, No. 3

STATEMENT OF OWNERSHIP, MANAGEMENT, AND CIRCULATION
(Act of October 23, 1962; Section 4369, Title 39, United States Code)

Date of Filing: November, 1979

Title of Publication: Iowa State Journal of Research

Frequency of Issue: Quarterly

Location of Known Office of Publication: South State Avenue, Ames, Story County, Iowa 50010.

Location of Headquarters of General Business Offices of the Publishers: South State Avenue, Ames, Story County, Iowa 50010.

Publisher: Iowa State University Press, Merritt Bailey, Business Manager, South State Avenue, Ames, Story County, Iowa 50010.

Editor: Duane Isely, 343 Bessey Hall, Iowa State University, Ames, Iowa 50011.

Owner: Iowa State University Press, Ames, Story County, Iowa 50010.

Known Bondholders, Mortgagees, and Other Security Holders Owning or Holding One Percent of More of Total Amount of Bonds, Mortgages, or Other Securities: None.

Extent and Nature of Circulation:

	Average no. copies each issue during preceding 12 months	Actual no. copies of single issue published nearest to filing date
A. Total no. copies printed (Net Press Run)	675	675
B. Paid circulation		
1. Sales through dealers and carriers, street vendors, and counter sales	450	450
2. Mail subscriptions	120	120
C. Total paid circulation (Sum of B1 and B2)	570	570
D. Free distribution by mail, carrier or other means samples, complimentary, and other free copies	0	0
E. Total distribution (Sum of C and D)	570	570
F. Copies not distributed		
1. Office use, left over, unaccounted, spoiled after printing	105	105
2. Returns from news agents	0	0
G. Total (Sum of E, F 1&2)	675	675

I certify that the statements made by me above are correct and complete.

Merritt Bailey
Business Manager

PALEOAGROSTOLOGY: A HISTORICAL REVIEW^{1,2}

Joseph R. Thomasson³

ABSTRACT. Recent work in paleoagrostology indicates that the descriptions of most fossils described as grasses before 1928 were based on little, if any, factual evidence. Many previously described genera of fossil grasses, including the invalid but widely used genus *Poacites*, should be abandoned. General macromorphological systems of identification of supposed fossil grass remains are not satisfactory, especially for leaf remains; it is suggested that modern micromorphological methods be used to rectify this situation. Recent data concerning the phylogenetic significance of micromorphological characters of leaf fragments and floral bracts of fossil grasses are reported.

INTRODUCTION

Paleoagrostology is young and prior to the studies of Elias (1932, et seq.) was based on little factual evidence. The early lack of factual knowledge is explained by two main factors. First, the classification of extant grasses was hardly adequate when the first description of a supposed fossil grass appeared in 1820. It would hardly be expected that fossil grasses, whose relationships were even more obscure, could be placed satisfactorily in the existing classification scheme. Second, and possibly most significantly, many of the fossils were impressions or compressions, and very little but a general, linear grasslike form was available for identifications. Because of these factors, it is not surprising that many of the early reports have been a source of continuing confusion.

The only previous reviews of paleoagrostology have been of a general nature (Gardner, 1886; Elias, 1942), and no comprehensive survey has been published. What follows is a review of paleoagrostology from 1820 to the present. Fossil grass genera discussed in this review are summarized in the appendix.

THE 1820-1927 PERIOD OF INVESTIGATION

The first account of fossil grasses is that of Schlotheim (1820). He described Paleozoic leaves, stems, and inflorescences, which had been preserved as impressions. For these, he erected (without description) the genus *Poacites*. Comparing his fossils to such extant genera as *Poa*, *Milium*, and *Phalaris*, Schlotheim was not completely convinced that these were truly grasses. I have seen the plates of Schlotheim's *Poacites zaeiformis*, and they cannot be assigned with any certainty to the Gramineae. Indeed, this species was assigned by Potonié (1893) to *Equisetites*, a form genus designated for fossils bearing a resemblance to recent species of *Equisetum*. Considering the Paleozoic age of the fossils, no doubt remains that Schlotheim's species of *Poacites* are not true grasses.

¹Journal Paper No. J-9443 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Project 1833.

²This paper is based upon a portion of a doctoral dissertation submitted to the Graduate College of Iowa State University in partial fulfillment of the Ph.D. degree in plant taxonomy.

³Associate Professor of Biology, Division of Science and Mathematics, Black Hills State College, Spearfish, South Dakota 57783

Brongniart (1822) may be regarded as having first validated the genus *Poacites* in his "Sur la Classification et la Distribution des Végétaux Fossiles en Général." Brongniart's work was accompanied by both a generic description, "Linear leaves with parallel nerves," and an illustration of a single species, *Poacites carinata*. It was also in this work, (Brongniart, 1822) that he first published a classification of all plant fossils, a basic outline of which follows:

CLASSIFICATION OF THE VEGETABLE FOSSILS

- I. Class 1. Stems whose internal organization is recognizable
- II. Class 2. Stems whose internal organization is not very distinct, but which are characterized by their external shape
- III. Class 3. United stems and leaves, or isolated leaves
- IV. Class 4. Fruiting organs

This classification was entirely artificial, as were the genera proposed in it. *Poacites* was placed by Brongniart in his Class 3. He made no attempt to define the genus with the Gramineae. This is clearly shown in the following statements:

Poacites, which apparently belongs to the monocotyledon plants, could come from plants of many different families. The characters which they offer up to the present are not sufficient to allow us to fix their (taxonomic) position in the plant kingdom; . . . we already said that these plants (fossil *Poacites*) belong to the monocotyledon plants, but it is not possible at the present to fix the family to which we should assign them.

Brongniart continued to use this generic concept of *Poacites* (Brongniart, 1825) when he described *Poacites yuccaeifolia*, inferring a resemblance to the genus *Yucca* of the Agavaceae. Even here the tenuous systematic nature of the genus *Poacites* is evident, as there is little, if any, evidence in the illustration and description provided with which one could taxonomically defend such an interpretation.

Culmites, another genus frequently mentioned in paleoagrostological works, was established by Brongniart (1822) for "Smooth, jointed stems, a single scar at each node" and placed in his Class 2. He illustrated and described a single species, *Culmites nodosus* Sternb. Although he noted that fossils of this species were similar to many Gramineae, he was uncertain of their exact relationships (Brongniart, 1822, 1825).

Brongniart later (1828a, 1828b) elaborated his earlier classification, placing the genera *Poacites* and *Culmites* in a section entitled "Monocotyledons whose family cannot be determined." Of *Poacites* he says "Among the (fossil) leaves, we ought to leave in this group monocots which cannot be identified, including most of the leaves (previously) designated by the name *Poacites*"; of *Culmites*, "These are jointed or sometimes branched, smooth or irregularly striated stems which have one to many scars of insertion at each node. . . , as for the families from which these stems come—they are numerous. . . ." The families he mentioned as possibilities were Gramineae, Cyperaceae, Juncaceae, Orchidaceae, and Canaceae. Brongniart (1828a) transferred the type species of *Poacites*, *P. carinata*, to the genus *Lepidophyllum*, far removed taxonomically, phylogenetically, and geologically from the monocotyledons. Since his decision was taxonomically sound, the name *Poacites* was no longer available for supposed fossil grasses.

Contemporaneous with Brongniart, Sternberg published his "Flora der Vorwelt" (1820-1838), which is now considered the nomenclatural starting point for fossil plants. In this series, he mentioned several genera whose names have appeared in later paleoagrostological publications. Aside from the importance of "Flora der Vorwelt" for paleoagrostological priority, it clearly illustrates the nebulous nature of many of the genera described during the early period of paleoagrostology. For example, Sternberg (1823) provided no illustra-

tions of *Poacites*, describing the genus as, "linear shaped leaves with parallel nerves, probably monocot plants." Later Sternberg (1825) established the genus *Bajera* and assigned it to his Ordo (presently family) Equisetaceae. An examination of the pertinent descriptions and plates indicates they are not grasses. In this same work Sternberg cited *Culmites* as a genus belonging to the Equisetaceae. As a final example, Sternberg (1825) described the genus *Volkmannia* with two species under his class Acotyledones, Order Najadcaeae. Of this genus he said "Essential characters. Striated, jointed stems. Spike-shaped inflorescence. A genus of plants transitional between Equisetaceae to Gramineae." The specimens illustrated, certainly not grasses, are possibly fossil Sphenophyta.

Lindley and Hutton (1831-1837) produced the first important paleobotanical work to appear in the English language. Among the genera they mentioned that are of significance in paleoagrostology are *Culmites*, *Poacites*, and *Volkmannia*. In volume one (1832) they presented a classification "Genera of Fossil Plants," giving the diagnostic characters of each of these genera. That portion important to this discussion is:

MONOCOTYLEDONOUS PLANTS OF DOUBTFUL AFFINITY

Stems only known.

Genus 50. *Culmites*. Stems articulated, with two or more scars at the joints. Three species—in the Tertiary beds.

Leaves only known.

Genus 52. *Poacites*. All Monocotyledonous leaves, the veins of which are parallel, simple, of equal thickness and not connected with transverse bars. Several species—in the Coal Formation. . . .

PLANTS, THE AFFINITY OF WHICH IS ALTOGETHER UNCERTAIN

Genus 89. *Volkmannia*. Stem striated, articulated. Leaves collected in approximated dense whorls. Three species—in the Coal formation.

Obs. These are possibly the leaves of *Calamites*.

Of the two species of *Volkmannia* that had been described by Sternberg, *Volkmannia polstachya* Sternb. was placed in synonymy with the Equisetaceous *Calamites nodosus* Schloth. I have examined both plates (Sternberg, 1823, Tab. 51, Fig. 1; Lindley and Hutton, 1832, pl. 15, Fig. 1) and, although I am not convinced that they are identical, there is no doubt that the fossils are related to the Equisetaceae, bearing no resemblance to the Gramineae. The remaining species, *Volkmannia distachya* Stern., was left in *Volkmannia* by Lindley and Hutton (1832), but the genus was placed among genera of fossils, "plants, the affinity of which is altogether unknown." Lindley and Hutton's concepts of *Poacites* and *Culmites* were broadly inclusive of many families of supposed monocot fossils. In 1833 they described *Poacites cocoina* as the "leaf of some pinnated palm, whose pinnae are of considerable width, as in many species of *Cocos*."

The next contribution that bears on the history of paleoagrostology is that of Braun (1840). In his catalogue of fossils deposited in the Bayreuth Museum, Bavaria, listed under a subheading "Plantae vasculares monocotyledonae," is the heading Graminites, with four genera: *Germaria*, *Poacites*, *Cyperites*, and *Zosterites*. Graminites presumably infers some similarity with the Gramineae, perhaps in the linear leaves, but Braun provided no description. This graminaceous relationship, however, seems evident from the several species of *Poacites* named by Braun; i.e. *P. phragmites*, *P. arundo*, *P. paspalum*, and *P. nardus*. The interpretation of *Poacites* by Braun is, like that of Schlotheim, not an exact statement that these fossils belong to the Gramineae, but only that they are similar. I have not resolved the

problem of his placement of the genera *Zosterites* and *Cyperites* in the (? Family) Gramin-ites. *Germaria*, established earlier by Presl (in Sternberg, 1838), does not belong in the Gramineae. The genus *Grammophyllum*, first published here by Braun (1840) as a *nomen nudum*, is not a fossil grass. It was placed in his (? Family) Cycadeaceites, a group related to the modern Cycadaceae, but which at the time he considered as belonging to the Monocotyledons.

The next significant contributions to paleoagrostology were made by Unger, a European botanist and paleontologist. In his "*Synopsis Plantarum Fossilium*" published in 1845, and followed by "*Genera et Species Plantarum Fossilium*" published in 1850, he attempted to bring together systematically all the known taxa assignable to the fossil Gramineae. A comparison of his classifications pertinent to this discussion follows.

<u>1845</u>	<u>1850</u>
Regio II Cormophyta	Regio II Cormophyta
Sectio IV Amphibrya	Sectio IV Amphibrya
Classis XIII Glumaceae	Classis XIII Clumaceae
Ordo XXXII Gramineae	Ordo XXXII Gramineae
Genus <i>Culmites</i>	Genus <i>Culmites</i>
Genus <i>Bambusium</i>	Genus <i>Bambusium</i>
Genus <i>Triticum</i>	Gramineae Dubiae
Gramineae Dubiae	Genus <i>Bajera</i>
Genus <i>Bajera</i>	Genus <i>Poacites</i>
Genus <i>Poacites</i>	Ordo XXXIII Cyperaceae
Genus <i>Cyperites</i>	Genus <i>Cyperites</i>

Among significant changes in classification proposed by Unger as compared with earlier authors is the placement of *Culmites* in the Gramineae and the establishment of an informal assemblage, "Gramineae Dubiae," to include *Poacites* and *Bajera*. Heer (1855) placed the single described species, *B. sepultum* Unger, in synonymy with his *Arundo goepperti* Heer. No evidence was given by Unger for classifying any of these fossils in the Gramineae.

During the period between Unger's initial (1845) and final (1850) classifications, Brongniart (1849) elaborated the classification of all fossil plants that he had initiated in 1822 and summarized the known fossil grasses:

As for *Poacites* the species which have been previously described are not only strangers to the grasses, but to the true monocotyledons as well. . . . , the plant named by Sternberg as *Bajera scanica*, and placed in the grasses by Unger, is also an unidentifiable monocot stem. . . . , as for stems previously designated as *Culmites*, they appear to be strangers to the grasses.

He left no doubt about the questionable nature of all the fossils previously assigned to the Gramineae.

In summary, by 1850 paleoagrostology had become firmly established in the paleobotanical literature, chiefly under the leadership of Brongniart. His initial work (1822) presented a classification of vegetative fossils, including any probable grasses, which was highly artificial and implied no natural relationships, but by 1849 he had elaborated it into a system of classification that was at least partly natural. He and his contemporaries were undoubtedly influenced by the revolution in the classification of extant plants occurring at the time. But even by 1850 no undoubted fossil grasses had been described.

Although the first half of the nineteenth century had produced a meager start for paleoagrostology, the second half provided an outpouring of literature. With these contribu-

tions came the first reports of fossil grasses from North America. In Europe, focus shifted from the Paleozoic coal formations to the Cenozoic strata. In elaboration of taxonomic systems, the relationships of supposed fossil grasses to their modern counterparts were elucidated.

At the beginning of this period, Otto (1854) erected the new genus *Arundinites* to include stem fragments similar to *Arundo*. There is no evidence to indicate that his fossils are grasses.

In the first and third volumes of his famous "*Flora Tertiaria Helvetiae*," Heer (1855, 1859) illustrated a large number of supposed fossil grasses. Species described include those from extant genera such as *Oryza*, *Panicum*, *Arundo*, and *Phragmites*, as well as the fossil genus *Poacites*. All specimens were from the Miocene-Pliocene strata of Europe. Some of the best illustrated of these are *Panicum trogloditarum* Heer (Heer, 1855; Tab. XXV, Fig. 2) and *Poacites schimperii* Heer (Heer, 1859; Tab. XXV, Fig. 7), and these, among others, are worthy of further study to determine if they are indeed fossil grasses. These early works of Heer expanded the definition of *Poacites* to include the stems and spikelets of Gramineae. No less than 16 new species of *Poacites* were described on the basis of leaves, stems, and spikelets.

Saporta's studies (1861, 1862b, 1863, 1865a, 1865b, 1867, 1873a, 1888, 1894) contain references to fossil grasses, or at least to grasslike fossils. These references mostly deal with Tertiary strata in which true grasses might today be expected to occur. Although Saporta's initial descriptions of a number of fossil grasses were made in 1861, it was not until 1862 that the first illustrations were provided. A number of species of the genus *Poacites* were described on the basis of leaf and "seed" fragments, and Saporta compared these purported fossil grasses to a number of living genera, including *Avena*, *Triticum*, *Poa*, *Lolium*, *Festuca*, and *Arundo*. Nevertheless, while some of the fossils (Saporta, 1862b, pl. 3, Figs. 12, 13, 14, 15) do resemble the spikelets of many Gramineae, they can hardly be identified with any final assurance.

Two sources of confusion in the literature must be clarified. First, Saporta (1861) published his initial work as a section in Heer (1861). In later works he refers to this as "Ex. anal." or "Examen analytique" when citing references to previous descriptions of species. Unfortunately, he did not use the original page numbers of Heer, but rather renumbered the pages for his section. For example, in describing *Rhizocaulae* (1862b, p. 193), pages 133-135 of Heer (1861) are cited by Saporta as "Examen analytique," p. 17-19. Second, in describing his species in later work, Saporta (1873a) again cited references to them as "Et. sur la veg. tert.," which refer to his series of studies entitled "*Etudes sur la végétation du sud-est de la France à l'époque tertiaire*." By using the citations of page numbers as he gave them, it is impossible to find those page numbers in the earlier literature. For example, in 1873a (p. 23) he cited under *Poacites glumaceus* Sap. a reference to "Et. sur la veg. tert., I, p. 66." Saporta's second "Etudes" study (1862b) begins on page 191 and concludes on page 311. Although there is a *Poacites glumaceus* Saporta in the latter paper, it is on page 219, not 66. If, however, one combines the pages of Saporta, 1862a and 1862b, and then renumbers them beginning with 1, then *Poacites glumaceus* is indeed found on page 66! This procedure is successful with all such citations throughout Saporta's "Etudes."

Rhizocaulon, a genus proposed by Saporta (1861), was described by him as including:

The monocotyledons of uncertain affinity which compose this group are still imperfectly known. Their structure indicates plants intermediate between the Cyperaceae, Restionaceae and Eriocaulaceae of our day.

I mention this genus because Andrews (1970) listed it as ? Gramineae. It was certainly not originally proposed as a fossil grass genus, and the illustration Saporta later (1862b) provided does not support such a conclusion. In this same work (1862b), he also

described *Panicum minutiflorum* Saporta, a later homonym of *Panicum minutiflorum* (Beauv.) Raspail, which cannot be classified unambiguously in the Gramineae. Marion (1872) later placed it in synonymy with *Podostachys minutiflora*, a fossil species of the Centrolepidaceae. Present-day members of this family are Asian and Australian grass-like monocots in which the flowers are subtended by glume-like bracts. *Panicum pedicellatum* illustrated by Saporta (1867, p. 53, pl. 3, Figs. 12, 13) is very similar to these and does not seem to be a grass.

Other genera of historical significance to paleoagrostology figure in a number of works by Saporta. The genus *Arundinarites* (Saporta, 1862) included "grasses" similar to the genus *Arundinaria*. The description given by him might fit any number of plants in many families. *Phragmites provincialis*, originally described by Saporta in 1861 but first illustrated in 1867, also is not taxonomically defensible. Indeed, Saporta later (1873b) established the genus *Pseudophragmites* to include this species, placing the genus in the family Rhizocaulaceae, a monocotyledon family appropriately labeled by Schimper (1870) as "familia sedis incertae." Saporta noted a faint resemblance of *Pseudophragmites* to the Gramineae in general, but again his illustration (1873b, p. 14, Fig. 1) could be that of any number of rhizomatous plants.

Saporta (1888) continued his use of *Poacites* as a genus of the Gramineae, describing and illustrating no less than 12 new species on the basis of spikelets, culms, and leaves. Of these, none presently can be definitely placed in the Gramineae. *Graminophyllum*, a fossil grass genus established earlier by Conwentz (1886), was referred by Saporta to synonymy under *Poacites*.

Saporta's last work (1894) also treated fossil grasses, returning to a conception of *Poacites* much closer to the original one of Brongniart than he had used in all previous studies. Of *Poacites*, he says (p. 57), "We conserve this name for grasslike, monocotyledon leaves, which are more or less comparable to those of the Gramineae, the Cyperaceae and certain Potamogetonaceae." In this same work Saporta also proposed the new genus *Phyllotaenia*, combining the fossil genera *Bambusium* and *Caulinites* (see Hollick, 1897b). His description, "For these we propose *Phyllotaenia*, which alludes to the ribbonlike shape of these types of leaves, whose real affinity escapes us," is very similar to the description Brongniart presented 75 years earlier for *Poacites*.

The name *Graminites*, originally proposed as a *nomen nudum* without specified rank by Braun (1840), was later validated by Geinitz (1865). Geinitz described and illustrated a single species, *Graminites feistmanteli*, from fossils found in Paleozoic coal deposits and proposed, "This may be the first grass (fossil) that has been found in the bituminous coal formation." There is no convincing evidence that his illustration, representing a culm with a few leaves attached, is a grass. Additionally the Paleozoic age of *Graminites* discredits its proposed affinities.

Ettingshausen (1866) presented a significant paper that dealt primarily with the nervation of extant grasses. The importance of his work as it bears on paleoagrostology, however, lies in an "Übersicht der fossilen Gramineen", which includes a systematic compilation of many fossil "grass" species and bibliography. It also contains the first report of the grass genera *Uniola* and *Arthrostylidium* in the fossil record.

Although the preponderance of the research in paleoagrostology during the 1860s and 1870s was in Europe, there was a developing literature in North America. Fossil grasses had been noted as early as 1859 (Engelmann, 1876) in the Tertiary of Nebraska, but a report by Newberry (1868) of a *Phragmites* sp. from the late Tertiary beds near Fort Union, Dakota (South Dakota) seems to be the first specific report of a presumed fossil grass from North American strata. The leaves, not illustrated, were fragments of a parallel-veined leaf, and Newberry provided no evidence to confirm his diagnosis.

Shortly afterward, Lesquereux, in a series of papers on the fossil floras of Tertiary and Cretaceous strata of the western and midwestern United States (1868, 1872, 1874, 1876a, 1876b, 1878) reported several fossil grasses, his 1878 paper perhaps being most sig-

nificant. Lesquereux said that "Gramineae and Cyperaceae are as yet poorly represented in the North American Tertiary flora; not so much on account of the deficiency of specimens as from the impossibility of determination of fragments of leaves or blades whose reference, even generic, is always problematic." Lesquereux was eventually convinced that such "positive characters," as "those of seeds with glumes and pallets" were necessary for adequate diagnosis of fossil grasses. Although such structures illustrated by him (1878, pl. 8, Figs. 7, 9) may not be grasses, his work represents a significant step towards the use of more reliable characters in identifying fossil grasses. Of all the fossil species he described, none can be positively identified as a grass.

Contemporaneously, Schimper (1870-72) published important European studies, which included a compilation of all known information on purported fossil grasses. An outline of his classification is:

- Class I Glumaceae
 - Ordo I Gramineae
 - Family I Oryzeae
 - Genus *Oryza* (1 sp)
 - Family II Paniceae
 - Genus *Panicum* (7 sp)
 - Family III Arundinaceae
 - Genus *Arundo* (5 sp)
 - Genus *Arundinites* (4 sp)
 - Genus *Phragmites* (3 sp)
 - Family IV Festuceae et Similites
 - Genus *Poacites*
 - A. Folia et culmi (28 sp)
 - B. Spiculae (1 sp)
 - Genus *Uniola*
 - Family V Bambuseae
 - Genus *Bambusa* (1 sp)

He included the Family Rhizocaulae, described by Saporta (1861) as broadly encompassing fossil grasses and other monocots, as a "Familia sedis incertae" in the Ordo Cyperaceae.

Shortly after Schimper, Heer (1874) proposed the name *Hypoglossidium*, for "the remains of three types of monocots, of which only one can be closely determined." He thought perhaps one might be an "arundineous grass (*Bambusium*). Although the remains vaguely resemble glumes, there is no evidence that the fossils he illustrated belong in the Gramineae, and in fact Post and Kuntze (1904) later placed this genus in the Pinaceae.

Twelve years passed before the next significant work in paleoagrostology appeared. This work, authored by Gardner (1886) and appropriately named "Fossil Grasses," is a general account of the history of fossil "grasses" to that date. Although in many ways incomplete, it is nevertheless one of the most significant bibliographic references to the older literature on paleoagrostology. His few illustrations of grass-like remains from the Oligocene provide no certainty of their relationship to the Gramineae even though some are perhaps suggestive of *Briza*.

The same year, Conwentz (1886) proposed the name *Graminophyllum* for "the true leaf remains of grasses," indicating that this name was intended to replace in part the genus *Poacites*. Although there is no micromorphological evidence to support his systematic assignment, this fossil superficially is indistinguishable from many modern grass leaves (Litke, 1966, 1968). Significantly this is the first genus proposed specifically for fossil grass leaves from strata (Tertiary) likely to contain grass fossils. Another fossil mentioned by him, *Zeites succineus*, seemingly resembles a small corn cob of *Zea*! (See Weatherwax, 1954, for illustrations of various mineral deposits that have been described as fossil "corn cobs.")

A year later, Ettingshausen (1887a) proposed the genus *Bambusites* and described one species on the basis of indeterminable leaf fragments, possibly of monocotyledonous nature. That same year, on the basis of stem fragments, he (1887b) added yet another species to this genus, which again provided no definitive characters by which such an assignment could be justified.

Closing out the last half of the nineteenth century were two significant paleoagrostological reports. Hollick (1897a) reported a fossil grass from Staten Island, New York, on the basis of rhizome and stem fragments. Although excellently preserved, they are not adequate for generic determination; such fragments are best placed in a form genus, (Thomasson, 1976a). Later that same year, Hollick (1897b) reviewed the history of the genus *Caulinites*, a genus originally described by Brongniart for branched stem fragments of the family Nayaides (Zosteraceae). As with many of these form genera based on fragments, *Caulinites* has been placed in a number of systematic positions, including the animal kingdom (as a polyp)! Hollick concluded that, "organisms described under the genus *Caulinites* should be regarded as belonging to the rhizomes of grasses, sedges, or rushes, and it is unfortunate that the generic name implies relationship with the Naiadaceae." However, such rhizomes are also found in families such as Orchidaceae (Holm, 1929). I remain unconvinced of the relationship of *Caulinites* except that they are probably monocotyledons of some sort.

The first fossil "grass" described in the 1900s was *Yorkia gramineoides* (Wanner) Ward. The only characteristic of this Triassic fossil that might imply any relationship to the Gramineae was the presence of linear leaves (Ward, 1900; p. 254, pl. XXXIV, Fig. 4-6). Considering its age and general nature, there is no reason to consider this fossil as a grass.

Post and Kuntze (1904) attempted to index the genera of living and fossil plants and to provide, as completely as possible, the valid names and their synonyms. This is the first attempt to correct the nomenclature of fossil plant genera, including those of fossil grasses, according to any rule of priority.

Berry (1905) briefly summarized the occurrence of fossil grasses in the geologic strata and concluded that the grasses were absent from the fossil record in the Paleozoic, rarely present in the Cretaceous, but abundantly represented in the Tertiary strata. Unfortunately, he provided no evidence to support this latter claim. Significantly, he did recognize that "*Poacites* as characterized by Brongniart in 1822 was monotypic, and his species having been relegated to synonymy, the name is not available for the Mesozoic species."

The years between 1906 and 1927 included numerous reports of fossil grasses. Cockerell (1908) described *Stipa laminarum* during a study of the fossil flora of the Tertiary Florissant Lake Beds, Colorado. This fossil was later (MacGinitie, 1953) determined to be a species of *Cercocarpus* (Rosaceae). In a short note, Brues and Brues (1908) described a specimen of *Melica primaeva*, also from the Florissant Beds. Beetle (1958) transferred this species to *Phalaris*, but I agree with MacGinitie (1953) and Anderson (1961) that the material is too poor to be identified. Penhallow (1908) reported fossil grass "seeds" from Tertiary strata in Canada but did not describe them. Five years later, Cockerell (1913) described *Phalaris geometrorum*, based on a structure vaguely resembling a glume; I agree with Anderson's (1961) rejection. Knowlton (1916) described *Mublenbergia florissantii* from the Florissant Beds, but MacGinitie (1953) later assigned this fossil to the genus *Stipa*. I have examined the type specimens of this species (USNM34750A, 34751), and believe the material is too poorly preserved to allow identification. Berry's (1918) treatment of fossil floras from Bolivia included descriptions and illustrations of species assigned to the genera *Festuca*, *Poacites*, and *Phragmites*. His evidence is insufficient to justify these determinations. Finally, in a catalogue of the fossil plants in the British Museum, Reid, Chandler, and Groves (1926) described and illustrated several plants that bear a nebulous resemblance to members of the Gramineae. They also proposed a new genus, *Monocotylophyllum*, "for monocotyledonous leaves of uncertain affinity."

In summary, the period of paleoagrostology from 1820 to 1927 was one in which

the number of genera and names of new fossil grass species greatly expanded, with little firm evidence for their supposed relationships.

1928 AND AFTER

This is the current period, during which fossil grass floral bracts (the lemma and palea together are called the anthoecium) assignable without doubt to the Gramineae were initially described. Also, the recent use of micromorphological methods has allowed accurate identification of cuticular and epidermal characteristics in the determination of true grass fossils from fragments that previously had been placed in genera such as *Poacites*.

The 13 years from 1928 to 1942 might be called the most fruitful in paleoagrostology, for it was during this period that Maxim K. Elias, the father of modern paleoagrostology, pioneered the study of fossil grasses and other herbs from the High Plains Tertiary of North America. Although Elias (1932) was the first person to recognize the High Plains fossils as grasses, he was not the first to collect them, nor even the first to describe them. It is now known that C.B. Hatcher made collections in 1884 of fossil "seeds" at the famous Sternberg Quarry in Phillips County, Kansas. Among them were the first undoubted fossil grasses, preserved as anthoecia. It was not until 45 years later that these fossils were described, and even then they were assigned to the Boraginaceae (Berry, 1928).

Elias (1932) described fossil plants from the Tertiary of Kansas and Colorado. He recognized several of the fossils described by Berry as true Gramineae. He characterized a new genus, *Berriochloa*, with two species which was said to resemble *Hordeum*. In addition, species of *Stipa* and *Panicum* were mentioned for the first time, and Elias noted that their perfect preservation allowed a close comparison with living forms. Fossils described under *Stipa* were later transferred to a new genus, *Stipidium* (Elias, 1935).

Elias, continuing studies of fossil grasses (1934, 1935, 1941), culminated in a systematic monograph of the fossil grasses (1942) of the High Plains Tertiary. He described two new genera, *Paleoeriacoma* and *Clementsella*, and discussed the phylogenetic relationships of previously described High Plains grass fossils to modern taxa. Though some of his conclusions are now dated, his work remains a paleoagrostological classic and should be consulted by anyone interested in the evolution of grasses.

Contemporaneously, other papers appeared (Berry, 1929, 1937; Frenguelli and Parodi, 1941, among others) that treated suspected fossil grasses. That of Frenguelli and Parodi is most interesting because it describes a supposed fossil bambusoid grass, *Chusquea*. None of these reports, however, provide sufficient evidence for the undoubted assignment of the fossils in the Gramineae.

The next significant paleoagrostological paper is that of Weyland (1957), who studied cuticular characteristics of some Tertiary monocots and initiated attempts to identify, by microscopic characters, plants that in the past had been placed in such dubious genera as *Poacites*. Noting that the epidermal features of both the Cyperaceae and Gramineae are similar and distinctive when compared with other plants, he established the genus *Glumophyllum* for "Not closely identifiable fossil leaf remains, that could come from the Gramineae as well as the Cyperaceae and show characteristics of recent types of these families." Citing Grob (1896) and Pfeiffer (1927), he indicated that the occurrence of the various cell types in long rows was considered by him to be diagnostic of both families, but only in rare cases could they be segregated.

Somewhat later, Ruffle (1963) described the micromorphological characteristics of a number of Tertiary monocot leaf fragments and concluded that they were from members of the Gramineae, on the basis of "The rows of stomata and long cells in combination with the short and long cells." The species described and illustrated were assigned to *Graminophyllum* proposed earlier by Conwentz (1886). Of the specimens illustrated, *Graminophyllum concavum* seems without any doubt to be a grass.

Litke (1966), describing three species of *Graminophyllum* and two of *Glumophyl-*

lum, similarly used micromorphological characters to determine the systematic position of fossil grass-like epidermal fragments. These fossils seem in systematic harmony with the characters of the fossil genera in which they were placed.

Most recently, Litke (1968) has examined the status of previous determinations of Tertiary fossil grasses which have been identified by epidermal characters as belonging to the Gramineae. He pointed out that remains of fossil grasses identified by Rüffle (1963) as *Glumophyllum ellipsoideum* and *G. amphistomatosum* were, in reality, palms. In addition, he reviewed the diagnostic characteristics of *Graminophyllum*; i.e., the presence of short and long cells, frequently in rows, the occurrence of silica-suberin couples, and the presence of dumbbell-shaped stomatal apparatus. He described and illustrated several new species of *Graminophyllum*.

Concomitant (1957-1968) with the epidermal analysis of fossil grasses other paleo-agrostological reports of a more traditional macromorphological nature appeared. Several of these (MacNeal, 1958; Chaney and Axelrod, 1959; Andreanszky, 1959; and Weyland, 1964), contain only general references to fossil grasses or describe linear leaf fragments, which were variously assigned to such genera as *Arundo*, *Phragmites*, and *Poacites*. Leonard (1958) described *Panicum eliasi*, from the High Plains of Texas, which is undoubtedly a grass fossil. Beetle (1958) transferred two fossil grasses previously described as *Melica primaeva* Brues and Brues and *Muhlenbergia florissanti* Knowlton, to *Phalaris primaeva* (Brues and Brues) Beetle and *Piptochaetium florissanti* (Knowlton) Beetle, respectively. As noted before, the material from which these fossils were originally described is poor, and the assignment of them to the Gramineae, at least on the basis of gross morphological characters, is entirely unwarranted. Sahni (1964), revising Indian monocotyledon fossils also defined *Poacites*: "A comprehensive artificial genus including impressions of grass-like leaves whose exact affinities are unknown. Veins parallel, unequal; transverse veins absent." Except for the reference to grass-like leaves, this definition is almost exactly that of Brongniart 142 years earlier. Finally, in 1966 Lancucka-Srodoniowa described a Miocene flora from Poland, which included reference to several grass "fruits." However, the illustrations provided of "small elongate remains, strongly flattened, at one end more or less rounded and at the other end distinctly pointed" are not convincing evidence for this assignment. Also in this report, specimens determined to be those of a species of *Panicum* by Rüffle (1963) were transferred to the genus *Ruppia* (Zosteraceae).

Frye and Leonard (1957, 1959, 1964), Leonard and Frye (1978), and Frye, Leonard and Swineford (1956) produced various, essentially geological reports that expanded the known geographical and stratigraphical distribution of fossil grasses in the High Plains Tertiary strata of North America.

Becker has recently reported a number of supposed fossil grasses from the Oligocene-Miocene Beaverhead Basins in southwestern Montana. Among the fossils described are spikelets and leaf fragments (1969) and inflorescences (1973). Of the leaf fragments, little can be said except that they are parallel-veined. His assignment of the fossils to the genera *Arundo* and *Phragmites*, as he notes himself, is tenuous. I do not believe that the fossil "spikelet," which he identified as *Agrostis*, belongs to the Gramineae. Although the structures shown by the fossil might be glumes, they might also be sepals or petals of some member of the Juncaceae. Even if they were glumes, the structure visible in the center could very well be the remains of the palea and lemma (anthoecium) and not the caryopsis, as he reported. Recently, Becker (1973) described the inflorescence of a fossil grass, *Graminites andropogonoides*, which he thought to be related to the modern *Andropogon scoparius* Michaux. This fossil deserves further study to determine if micromorphological characters have been preserved.

Galbreath (1974) reported a *Stipideum* [sic] from the Oligocene White River Formation, which, if correctly dated, represents a significant older extension of the known geologic occurrence of the High Plains Tertiary grasses. A study by Palmer (1976) using Pleistocene grass cuticles as a paleoecological tool is notable as a demonstration of the potential

use of the microfeatures of grass fossils. My report of a cyperaceous rhizome (Thomasson, 1976a) notes the presence of several fossil grasses in the same stratum.

I have reported on fossil grasses in the vicinity of vertebrate faunas in Nebraska (Thomasson, 1977) and Kansas (Thomasson, 1979b). Leonard and Frye (1978) have described the occurrence of fossil grasses in Tertiary strata of New Mexico. Most recently, I have shown the evolutionary significance of the epidermal features of the lemma and palea in fossil and living grasses (Thomasson, 1976b, 1978a, 1978b, 1979a). Such features seem to be an unexploited systematic character worthy of more detailed studies. This is especially true of fossils from the Tertiary deposits of North America because of their abundance and excellent preservation.

CONCLUSIONS

Paleoagrostology might be said to have gained reliability during the period 1928-1979. During this period, the first undoubted fossil grasses were described on the basis of fossilized anthoecia, and micromorphological investigation began to bring taxonomic clarity exceeding previous nebulous reports.

The genus *Poacites*, which has been a source of confusion throughout the history of paleoagrostology, should be dropped from further consideration in the taxonomic literature. It is obviously not available for further use since in its original description by Brongniart it was monotypic and the single species placed there was identified later (Brongniart, 1828a) as a *Lepidophyllum*. Its subsequent uses have been so varied that it is, for all practical purposes, meaningless. Of the genera that have been proposed for fossil grasses before 1928, only *Graminophyllum* seems to have sufficient basis in fact, and is the only available legitimate name specifically for fossil grass leaves and fragments of cuticle (Litke, 1966, 1968; Thomasson, 1979a). Only a restudy of some of these early fossils, using micromorphological features might allow meaningful identification of some of them. Dilcher (1974) has previously advocated such an approach to the identification of all fossil angiosperm leaf remains. The assignment of many fragments on the basis of gross morphology to such living grass genera as *Arundo*, *Panicum*, *Phragmites*, and *Uniola* should be immediately abandoned.

ACKNOWLEDGMENTS

I wish to express my sincere thanks to Dr. Richard W. Pohl for his help and suggestions given to me in developing this review. The careful reading of this manuscript by Dr. Duane Isely, Dr. Nels Lersten, and Dr. Richard W. Pohl is very much appreciated.

The research that resulted in this manuscript was supported in part by NSF Grant BMS 74-13324. The facilities of the Iowa State University Herbarium were used in the preparation of this paper.

LITERATURE CITED

- Anderson, D.E. 1961. Taxonomy and distribution of the genus *Phalaris*. Iowa State J. Sci. 36: 1-96.
- Andreanszky, G. 1959. Die Flora der sarmatischen Stufe in Ungarn. Akademiai Kiado, Budapest. 360 pp.
- Andrews, H.N. 1970. Index of generic names of fossil plants, 1820-1965. U.S. Geol. Surv. Bull. 1300: 1-354.
- Becker, H.F. 1969. Fossil plants of the Tertiary Beaverhead basins in southwestern Montana. Palaeontographica Abteilung B. 127: 1-142.
- . 1973. A new Tertiary gramineous fossil. Bull. Torrey Bot. Club 100: 318-320.
- Beetle, A.A. 1958. *Piptochaetium* and *Phalaris* in the fossil record. Bull. Torrey Bot. Club 85: 179-181.

- Berry, E.W. 1905. Fossil grasses and sedges. *Amer. Nat.* 39: 345-348.
- , 1918. Fossil plants from Bolivia and their bearing upon the age of uplift of the eastern Andes. *Proc. U.S. Natl. Mus.* 54: 103-165.
- , 1928. Fossil nutlets of the genus *Lithospermum*. *Proc. U.S. Natl. Mus.* 73: 1-3.
- , 1929. The fossil flora of the Loja Basin in southern Ecuador. *Johns Hopkins University Studies Geology* 10: 79-136.
- , 1937. Eocene plants from Rio Turbio in the territory of Santa Cruz, Patagonia. *Johns Hopkins University Studies Geology* 12: 91-97.
- Braun, F. 1840. Verzeichniss der in der Kreis-Naturalien-Sammlung zu Bayreuth befindlichen Petrefactern. Leopold Voss, Leipzig. 118 pp.
- Brongniart, A. 1822. Sur la classification et la distribution des végétaux fossiles en général, et sur ceux, des terrains de sédiment supérieur en particulier. *Museum Natl. Hist. Mém.* Paris 8: 203-348.
- , 1825. Note sur les végétaux fossiles de l'oolite à Fourgères de Mamers. *Ann. Sci. Nat.* 1st serie, 4: 417-423.
- , 1828a. Prodrôme d'une histoire des végétaux fossiles. F.G. Levrault, Paris. 238 pp.
- , 1828b. Végétaux fossiles. Pages 16-212 in F.G. Levrault, ed. *Dictionnaire des Sciences Naturelles*. Vol. 57. F.G. Levrault, Paris. 628 pp.
- , 1849. Végétaux fossiles. Pages 256-386 in A. Pilon, ed. *Dictionnaire universel d'histoire naturelle*. Vol. 14. D.E. Martinet, Paris. 604 pp.
- Brues, C.T., and B.E. Brues. 1908. A new fossil grass from the Miocene of Florissant, Colorado. *Wisconsin Nat. Hist. Soc. Bull.* 6: 170-171.
- Chaney, R.W., and D.I. Axelrod. 1959. Part II. Systematic considerations. Pages 134-229 in *Miocene Floras of the Columbia Plateau*. Carnegie Inst. Wash. Publ. 617. Washington. 229 pp.
- Cockerell, T.D.A. 1908. The fossil flora of Florissant, Colorado. *Amer. Mus. Nat. Hist. Bull.* 24: 71-110.
- , 1913. Fossil flowers and fruits-III. *Torreyia* 13: 75-77.
- Conwentz, H. 1886. Die flora des Bersteins und ihre Beziehungen zur Flora der Tertiärformation und der Gegenwart. Vol. 2. Danzig, Poland. 140 pp.
- Dilcher, D. 1974. Approaches to the identification of angiosperm leaf remains. *Bot. Review* 40(1): 1-157.
- Elias, M.K. 1932. Grasses and other plants from the Tertiary rocks of Kansas and Colorado. *Univ. Kans. Sci. Bull.* 20(20): 333-367.
- , 1934. Zones of fossil herbs in the late Tertiary of the High Plains. *Geol. Soc. Amer. Proc.* 1934: 332. (Abstr.)
- , 1935. Tertiary grasses and other prairie vegetation from the High Plains of North America. *Amer. J. Sci.* 29: 24-33.
- , 1941. Late Tertiary prairie vegetation in Nebraska. Pages 19-20 and fig. 2 (opposite p. 6) in *Guide for a field conference on the Tertiary prairie vegetation in Nebraska*. Nebr. State Mus. Special Publ. No. 2.
- , 1942. Tertiary prairie grasses and other herbs from the High Plains. *Geol. Soc. Amer. Special Paper (Regular Studies)* 41: 1-176.
- , 1946. Taxonomy of Tertiary flowers and herbaceous seeds. *Amer. Midl. Nat.* 36: 373-380.
- Engelmann, H. 1876. Appendix I. Report on the geology of the country between Fort Leavenworth, Kansas and the Sierra Nevada, near Carson Valley. Pages 243-335 in *Simpson, J.H. Report of explorations across the Great Basin of the Territory of Utah for a direct wagon-route from Camp Floyd to Geneva, in Carson Valley, in 1859*. Govn. Print. Off. Washington. 518 pp.
- Ettingshausen, C.R. 1866. Beiträge zur Kenntniss der Nervation der Gramineen. *Kaiserlichen Akademie Wissenschaften Sitzungsburg* 52: 411-430.
- , 1887a. Beiträge zur Kenntniss Tertiärflorea Australiens. *Denkschriften Kaiserlichen Akademie Wissenschaften* 53: 81-142.

- , 1887b. Beiträge zur Kenntnis der fossilen Flora Neuseelands. Denkschriften Kaiserlichen Akademie Wissenschaften 53: 143-192.
- Frenguelli, J., and L. R. Parodi. 1941. Una *Chusquea* fósil de el Mirador. Notas Del Museo de la Plata: Paleontologia 6: 235-238.
- Frye, J.C. and A.B. Leonard. 1957. Studies of Cenozoic geology along eastern margin of Texas High Plains, Armstrong to Howard Counties. Univ. Texas Bureau Econ. Geol. Report Invest. 32: 1-62.
- , -----, 1959. Correlation of the Ogallala Formation (Neogene) in western Texas with type localities in Nebraska. Univ. Texas Bureau Econ. Geol. Report Invest. 39: 1-46.
- , -----, 1964. Relation of Ogallala Formation to the southern High Plains in Texas. Univ. Texas Bureau Econ. Geol. Report Invest. 51: 1-25.
- , -----, and A. Swineford. 1956. Stratigraphy of the Ogallala Formation (Neogene) of northern Kansas. Kans. Geol. Surv. Bull. 118: 1-92.
- Galbreath, E.C. 1974. Stupid grass "seeds" from the Oligocene and Miocene deposits of northeastern Colorado. Trans. Ill. Acad. Sci. 67: 366-368.
- Gardner, J.S. 1886. Fossil grasses. Geol. Assoc. (London) Proc. 9: 433-454.
- Geinitz, H.B. 1865. Über einige seltene Versteinerungen aus der unteren Dyas und der Steinkohlen-Formation. Neues Jahrbuch für Mineralogie, Geologie Paläontologie 35: 385-395.
- Grob, A. 1896. Beiträge zur Anatomie der Epidermis der Gramineenblätter. Bibliotheca Botanica 36: 1-123.
- Heer, O. 1855-1859. Flora Tertiaria helvetiae. 1: 1-117. 1855. 2: 1-110. 1856. 3: 1-377. 1859. Winterthur, Paris.
- , 1861. Recherches sur le climat et la végétation du pays tertiaire. Winterthur, Paris. 220 pp.
- , 1874. Die Kreide-flora der artischen Zone Kongl. Svenska Vetenskapsakad. Handlingar 12(6): 1-140.
- Hollick, A. 1897a. A new fossil grass from Staten Island. Bull. Torrey Bot. Club 24: 122-124.
- , 1897b. Affinities of *Caulinites* Ad Brong. Bull. Torrey Bot. Club 24: 582-584.
- Holm, Theo. 1929. The application of the term rhizome. Rhodora 31: 6-17.
- Knowlton, F.H. 1916. A review of the fossil plants in the United States National Museum from the Florissant lake beds at Florissant, Colorado. Proc. U.S. Natl. Mus. 51: 241-297.
- Lancucka-Srodoniowa, M. 1966. Tortonian flora from the "Gdów Bay" in the south of Poland. Acta Palaeobotica 7(1): 1-133.
- Leonard, A.B. 1958. Two new fossil plants from the Pliocene of Northwestern Texas. Univ. Kans. Sci. Bull. 38: 1393-1403.
- , and J.C. Frye. 1978. Paleontology of Ogallala Formation, northeastern New Mexico. New Mexico Bureau Mines, Mineral Resources, Circular 161: 1-21.
- Lesquereux, L. 1868. On some Cretaceous fossil plants from Nebraska. Amer. J. Sci. 46(136): 91-105.
- , 1872. Fossil flora. Pages 283-318 in F.V. Hayden, ed. Report (5th Annual) U.S. Geol. Surv. Territories (for 1871). U.S. Govn. Print. Off., Washington. 538 pp.
- , 1874. On the Tertiary flora of the North American lignitic, considered as evidence of the age of the formation. Pages 275-366 in F.V. Hayden, ed. Report (8th Annual) U.S. Geol. Surv. Territories. U.S. Govn. Print. Off., Washington. 508 pp.
- , 1876a. A review of the fossil flora of North America. U.S. Geol. and Geog. Surv. Territories 1(No. 5, 2nd Ser.): 233-248.
- , 1876b. On some new species of fossil plants of the lignitic formations. U.S. Geol. and Geog. Surv. Territories 1(No. 5, 2nd Ser.): 363-389.

- , 1878. Monocotyledones. Pages 85-91 in F.V. Hayden, Contribution to the fossil flora of the Western Territories. Part II. The Tertiary Flora. Report U.S. Geol. Surv. Territories Vol. 7. U.S. Govn. Print. Off., Washington. 366 pp.
- Lindley, J., and W. Hutton. 1831-1837. The fossil flora of Great Britain, or figures and descriptions of the vegetable remains found in a fossil state in this country. London. 1: 1-48. 1831; 49-166. 1832; 167-218. 1833a. 2: 1-54. 1833b; 57-156. 1834; 157-206. 1835. 3: 1-72. 1835; 73-122. 1836; 123-205. 1837.
- Litke, R. 1966. Kutikularanalytische Untersuchungen im Niederlausitzer Unterflöz. Paläontologische Abhandlungen B, Palaobotanik 2: 328-414.
- , 1968. Über den Nachweis tertiärer Gramineen. Monatsberichte Deutschen Akademie Wissenschaften Berlin 10(6): 462-471.
- MacGinitie, H.D. 1953. Fossil plants of the Florissant beds, Colorado. Carnegie Inst. Wash. Publ. 559: 1-198.
- MacNeal, D.L. 1958. The flora of the upper Cretaceous Woodbind Sand in Denton County, Texas. Monograph Acad. Sci. Philadelphia 10: 1-152.
- Marion, M.A.F. 1872. Plantes fossiles des Calcaires Marveux de Ronzon. Ann. Sci. Nat. Bot. 5th Serie, 4: 326-364.
- Newberry, J.S. 1868. Notes on the later extinct floras of North America, with descriptions of some new species of fossil plants from the Cretaceous and Tertiary Strata. Ann. Lyceum Nat. Hist. New York 9: 27-76.
- Otto, E. 1852-1854. Additamente zur Flora des Quadergebirges in der Gegend um Dresden und Dippoldiswalde. Pt. 1: 1-29. 1852?; Pt. 2: 1-53. 1854.
- Palmer, P.G. 1976. Grass Cuticles: a new paleoecological tool for East African lake sediments. Can. J. Bot. 54: 1725-1733.
- Penhallow, D.J. 1908. Report on Tertiary Plants of British Columbia. Can. Dept. Mines, Geol. Surv. Branch 1013: 1-167.
- Pfeiffer, H. 1927. Untersuchungen zur vergleichenden Anatomie der Cyperaceen. Bibl. Bot. Centbl. 44: 1-90.
- Post, T., and O. Kuntze. 1904. Lexicon generum phanerogamarum. Stuttgart. 714 pp.
- Potonié, R. 1893. Die Flora des Rothliegenden von Thüringen. (Th. I). Jahrbuch Kaiser Preussen Geologie Landesamt 9: 1-298.
- Reid, E., M.E.J. Chandler, and J. Groves. 1926. Catalogue of Cainozoic plants in the department of Geology. British Museum of Natural History—The Bembridge Flora. The Oxford Press, London. 206 pp.
- Ruffle, L. 1963. Die obermiozäne (sarmatische) Flora von Randecker Maar. Paläontologische Abhandlungen 1(3): 139-298.
- Sahni, B. 1964. Revisions of Indian fossil plants. Part III—Monocotyledons. Monograph Birbal Sahni Institute Palaeobotany 1: 1-89.
- Saporta, G. 1861. Examen des flores tertiaires de Provence. Pages 133-171 in O. Heer. Recherches climat et la végétation du pays tertiaire. Winterthur, Paris. 220 pp.
- , 1862a-1873b. Études sur la végétation du sud-est de la France à l'époque tertiaire. Ann. Sci. Nat. Bot. 4th Serie. 16: 309-345. 1862a. 17: 191-311. 1862b. 19: 5-125. 1863. 5th Serie. 3: 5-152. 1865a. 4: 5-264. 1865b. 8: 5-136. 1867. 9: 5-62. 1868. 17: 5-44. 1873a. 18: 23-146. 1873b.
- , 1888. Dernières adjonctions à la flore fossile d'Aix-en-Provence. Ann. Sci. Nat. Bot. 7th Serie, 7: 1-104.
- , 1894. Flore fossile du Portugal. Acad. Royale Sci. Lisbon. 288 pp.
- Schimper, W.P. 1869-1874. Traité de paléontologie végétale ou à flore du monde primitif. 4 Vols. J.B. Baillier et fils, Paris.
- Schlotheim, E.F. 1820. Die Petrefacten-kunde auf ihrem jetzig Standpunkte durch die Beschreibung seiner Sammlung versteinerter und fossiler Überreste des thür Pflanzensreichs der Vorwelt erläutert Gotha. lxii. 437 pp.
- Sternberg, G.K. 1820-1838. Versuch einer geognostischen botanischen Darstellung der Flora

- der Vorwelt. Vol. 1. Pt. 1: 1-24. 1820; Pt. 2: 1-33. 1822; Pt. 3: 1-39. 1823; Pt. 4: 1-48. 1825. Vol. 2. Pt. 5, 6: 1-80. 1833; Pt. 7, 8: 81-220. 1838. Tentamen. i-xxvi. 1825. Leipzig and Prague.
- Thomasson, J.R. 1976a. *Cyperacites richardsii* (Cyperaceae), a new fossil plant from the Pliocene of western Kansas. Amer. Midl. Nat. 95: 239-242.
- , 1976b. Tertiary grasses and other angiosperms from Kansas, Nebraska and Colorado: Relationships to living taxa. Ph.D. dissertation. Iowa State University Library. 411 pp.
- , 1977. Fossil grasses, borages and hackberries from southwestern Nebraska. Univ. Wyoming Contr. Geol. 16(1): 34-39.
- , 1978a. Observations on the characteristics of the lemma and palea of the late Cenozoic grass *Panicum elegans* Elias. Amer. J. Bot. 65: 34-39.
- , 1978b. Epidermal patterns of the lemma in some fossil and living grasses and their phylogenetic significance. Science 199: 975-977.
- , 1979a. Tertiary grasses and other angiosperms from Kansas, Nebraska and Colorado: Biostratigraphy and relationships to living taxa. In press, Kans. Geol. Surv. Bull. 218.
- , 1979b. Angiosperms from the late Tertiary Keller local fauna of Ellis County, Kansas. In press. Univ. Wyoming Contr. Geol.
- Unger, F. 1845. Synopsis plantarum fossilium. Leipzig. 330 pp.
- , 1850. Genera et species plantarum fossilium. Vienna. 627 pp.
- Ward, L.F. 1900. Status of the Mesozoic floras of the United States—The older Mesozoic. U.S. Geol. Surv. 20th Ann. Report (Pt. 2): 213-430.
- Weatherwax, P. 1954. Indian corn in old America. Macmillan, New York. 253 pp.
- Weyland, H. 1957. Kritische Untersuchungen sur Kutikularanalyse tertiärer Blätter III, Monocotylen der rheinischen Braunkohle. Palaeontographica Abteilung B, 103: 34-74.
- , 1964. Lehrbuch der Paleobotanik. Wiley, New York.

APPENDIX

This appendix chronologically summarizes information concerning the fossil genera discussed in this review. For each genus, the reference, date, and page of first effective (E) and(or) valid (V) publication is given; this is followed by an edited summary of the author's diagnosis. The appendix has been compared with the "Index of Generic Names of Fossil Plants, 1820-1965" prepared by Andrews (1970) and differences are noted in the remarks column. Other remarks are included in some instances.

<u>Genus</u>	<u>Publication</u>	<u>Original Description</u>	<u>Remarks</u>
<i>Poacites</i>	(E,V) Brongniart, 1822, p. 210.	Linear leaves with monocotyledon affinities.	The single species on which this genus was erected, <i>Poacites carinata</i> Ad. Br. was transferred to <i>Lepidophyllum</i> by Brongniart (1828a, p. 87).
<i>Culmites</i>	(E,V) Brongniart, 1822, p. 215.	Smooth, jointed stems with a single branch scar at each node; ? with monocotyledon affinities.	

<u>Genus</u>	<u>Publication</u>	<u>Original Description</u>	<u>Remarks</u>
<i>Bajera</i>	(E,V) Sternberg 1825, Tentamen p. xxviii.	Jointed stems.	Placed in Equisetaceae by Sternberg (1825,p.xxviii).
<i>Volkmannia</i>	(E,V) Sternberg, 1825, Tentamen p. xxix.	Striated, jointed stems with spikelike inflorescence.	Considered by Sternberg to be a transitional genus between Equisetaceae and Gramineae.
<i>Caulinites</i>	(E,V) Brongniart, 1828a, p. 115.	Branched stems with branch scars at each node.	Assigned to Nayades by Brongniart; not origin- ally described from a monocotyledon leaf as reported by Andrews (1970).
<i>Germaria</i>	(E,V) Presl, 1838 (in Stern- berg, 1838, p. 188).	Spike shaped inflorescences of uncertain affinities.	? Equisetaceae
<i>Graminites</i>	(E) Braun, 1840, p. 99.	Monocot (? leaves).	Nomen nudum.
<i>Grammophyllum</i>	(E) Braun, 1840, p. 100.	Cycad (? leaves).	Nomen nudum.
<i>Bambusium</i>	(E,V) Unger, 1847, p. 128.	Jointed stems bearing panicle like inflores- cence; with gramin- aceous affinities.	Originally appeared as a nomen nudum (Unger, 1845, p. 166).
<i>Arundinites</i>	(E,V) Otto, 1854, p. 27.	Stem fragments of unknown affinities.	
<i>Rhizocaulon</i>	(E,V) Saporta, 1861, (in Heer, 1861, p. 135).	Leaves and stems with monocotyledon affinities.	
<i>Arundinarities</i>	(E) Saporta 1862b, p.221.	Stems and rhizomes similar to those of <i>Arundinaria</i> .	Not definitely accepted by Saporta, i.e., " <i>Arund- inarites?</i> "
<i>Graminites</i>	(E,V) Geinitz, 1865, p. 392.	Grass culm with leaves.	From Paleozoic strata; found along with <i>Sigil- laria</i> .
<i>Pseudopbragmites</i>	(E,V) Saporta, 1873a, p. 30.	Monocotyledon (? Gramineae) leaf and rhizome frag- ments.	Synonym, in part, of <i>Rhizocaulon</i> .

<u>Genus</u>	<u>Publication</u>	<u>Original Description</u>	<u>Remarks</u>
<i>Hypoglossidium</i>	(E, V) Heer, 1874, p. 129.	Monocotyledon leaves.	Synonym, in part, of <i>Rhizocaulon</i> ; placed in Pinaceae by Post and Kuntze (1904).
<i>Graminophyllum</i>	(E,V) Conwentz, 1886, p. 15.	Grass leaves.	From Tertiary strata.
<i>Bambusities</i>	(E,V) Ettingshausen, 1887a, p. 95.	Monocotyledon leaf fragments (? <i>Bambusa</i>).	Synonym, in part, of <i>Rhizocaulon</i> .
<i>Phyllotaenia</i>	(E,V) Saporta, 1894, p. 216.	Ribbon shaped leaves of unknown affinity.	Saporta included <i>Bambusium</i> and <i>Caulinites</i> in this genus.
<i>Yorkia</i>	(E) Wanner, 1900 (in Ward, 1900, p. 254).	Grass leaves.	From Mesozoic (Triassic) strata; a synonym of <i>Graminophyllum</i> .
<i>Monocotylophyllum</i>	(E) Reid et al., 1926, p. 87.	Leaves with monocotyledon affinities.	Synonym, in part, of <i>Rhizocaulon</i> .
<i>Berriochloa</i>	(E,V) Elias, 1932, p. 347.	Grass hulls (lemma and palea).	
<i>Stipidium</i>	(E,V) Elias, 1935, p. 26.	Elongate, cylindrical, <i>Stipa</i> -like hulls.	Andrews (1970) incorrectly indicated valid publication as 1942. <i>Stipidium</i> is a synonym of <i>Berriochloa</i> (Thomason, 1979a).
<i>Paleoeriocoma</i>	(E,V) Elias, 1942, p. 100.	Grass hulls (lemma and palea).	
<i>Clementsella</i>	(E,V) Elias, 1942, p. 103.	Grasslike "fruit" with long awn.	Possibly fossil <i>Cercocarpus</i> (Rosaceae).
<i>Glumophyllum</i>	(E) Weyland, 1957, p. 42.	Leaf cuticle fragments of Gramineae or Cyperaceae.	Synonym, in part, of <i>Graminophyllum</i> .

ERAGROSTIS HONDURENSIS, A NEW GRASS
SPECIES FROM CENTRAL AMERICA
(Gramineae: Chloridoideae: Eragrosteae)¹

Richard W. Pohl²

ABSTRACT. *Eragrostis hondurensis* Pohl, sp. nov. is described. The species is similar to *E. viscosa*. It occurs in abundance in southern Honduras and has also been found in Nicaragua and Oaxaca, Mexico. Chromosome number $n = ca\ 20$.

ERAGROSTIS HONDURENSIS Pohl, sp. nov.

Gramen annuum *Eragrostin viscosam* (Retz.) Trin. culmis paniculisque viscidis simulans, ab ea pedicellis terminalibus longioribus 6–10 (nec 2–3) mm longis, spiculis linearibus, lemmatibus truncatis disarticulantibus ciliisque palearum brevioribus 0.2–0.3 (nec 0.5–0.6) mm longis recedit.

Plant annual, caespitose in small tufts, 25–65 cm tall, erect; culms branching from the middle and basal nodes; prophylla 7–18 mm long, tapered to a point; internodes cylindrical, glabrous, ca one mm thick, hollow, usually bearing a ring of linear, longitudinal, depressed, yellow glands below the nodes; nodes purple, glabrous, not prominent; culm leaves usually 2–3, their sheaths shorter than the internodes, keeled, bearing scattered elongated papillose-based hairs, especially near the margins and apex; ligule a densely white-ciliate, short membrane, 0.2–0.5 mm long; leaf blades glabrous, flat, up to 10 cm long, 2–4 mm wide; collar bearing a ring of elongated papillose-based hairs; dewlap purple; many parts of the plant viscid and with adhering soil particles. Peduncle exerted up to 14 cm, the peduncle and inflorescence usually making up more than half the height of the plant; panicles terminal on the main culm and on leafy branches, the terminal one 9–28 cm long, 3–10 cm wide, open-cylindrical; branches usually solitary, rarely 2–3 per node, spreading, to 6 cm long; axils of main and secondary branches bearing tufts of elongated papillose-based hairs; spikelets borne on divergent pedicels, the lateral ones 1.5–2.0 mm long, the terminal one 6–10 mm long. Spikelets laterally compressed, linear, 5.0–7.5 mm long, often purplish, disarticulating by dropping of the lemmas and eventually by the dropping of some of the upper florets; glumes subequal, keeled, acute, 1.2–1.7 mm long, one-nerved; florets 7–14; lemmas 1.4–1.5 mm long, oblong, the apex broadly truncate, surface and nerves scabrid; palea about equal to the lemma, the cilia of the keels 0.2–0.5 mm long; anthers 3, purple, 0.2–0.3 mm long; caryopsis elliptical, 0.5 mm x 0.3 mm, castaneous, translucent. Chromosome number $n = ca\ 20$, from a cultivated seedling of Pohl & Gabel 13442 (ISC); $2n = 40$ reported by Gould & Soderstrom, Can. J. Bot. 48:1635. 1970, sub *E. viscosa* (Retz.) Trin.

Dry *Acacia* savannas, pastures, abandoned fields, interior valleys of Honduras and northwestern Nicaragua; Oaxaca, Mexico; elevations 440–640 m.

This species is abundant in the valley of the Rio Choluteca north of Oropol, Honduras. It resembles the introduced Asiatic *E. viscosa* (Retz.) Trin. in its viscid culms and inflorescence but differs in the features cited in the chart. *Eragrostis glutinosa*

¹Journal Paper No. J-9698 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa. Project 1833.

²Department of Botany, Iowa State University, Ames, Iowa.

(Swartz) Trin. of Cuba and Jamaica is also glutinous, but is said to be perennial and differs from our species in its more numerous, very narrow, involute pubescent leaf blades and in spikelet size and proportions.

Character	<i>E. hondurensis</i>	<i>E. viscosa</i>
Leaf blades	glabrous	papillose-pilose
Lateral pedicels	1.5–2.0 mm	0.3–1.2 mm
Terminal pedicel	6–10 mm	2–3 mm
Spikelet length	5.0–7.5 mm	3.0–5.5 mm
Spikelet shape	linear	ovate
No. of florets	7–14	6–10
Disarticulation	lemmas dropping	florets dropping
Lemma apex	truncate	tapered but blunt
Palea cilia	0.2–0.5 mm	0.5–0.6 mm

HOLOTYPE: HONDURAS: Dept. El Paraíso: 10.5 km SE of Yuscarán, elev. 550 m, abandoned field near a small stream, 31 December 1977, *Pobl & Gabel* 13442 (ISC 329297).

OTHER SPECIMENS: HONDURAS: Dept. El Paraíso: 10.5 km SE of Yuscarán, 26 December 1978, *Pobl & Gabel* 13802 (Topotype)(ISC); Dept. El Paraíso, 15 km SE of Yuscarán, elev. 440 m, 26 December 1978, *Pobl & Gabel* 13805 (ISC). Dept. Comayagua: 4 km S of Comayagua, elev. 640 m, 19 December 1955, *Johannessen* 612 (US 2237528); MEXICO: Est. Oaxaca: 20 km W of Zantepec, 2n = 40, 8 October 1968, *Gould* 12768 (US 2594052) NICARAGUA: Dept. Nueva Segovia, dried up riverbed in deep ravine, 3 km W of Ocotal, 20 December 1968, *Seymour* 848

The Latin diagnosis was kindly revised by Dr. Rupert Barneby of the New York Botanical Garden.

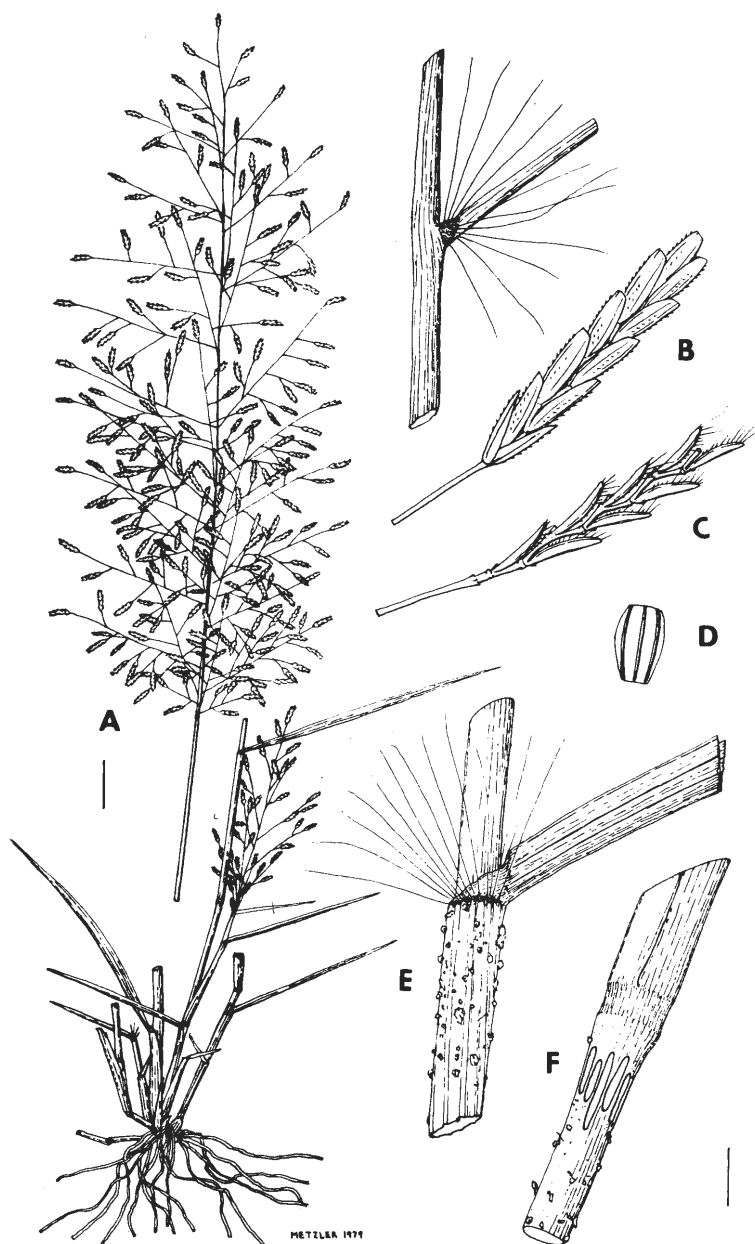


Figure 1. *Eragrostis bondurensis* Pohl, sp. nov. A. Plant B. Spikelet C. Spikelet with glumes and lemmas shed D. Lemma E. Leaf sheath with adherent soil particles F. Portion of internode with glands. Scale line for plant is 1 cm long; line for B–F is 1 mm long.

FLORA OF ADAK ISLAND, ALASKA:
LICHENS, LIVERWORTS, MOSSES

Michael K. Hein¹

ABSTRACT. Thirty-seven species of lichens, liverworts, and mosses are reported for Adak Island, Alaska. Of these, ten species are new reports for the Aleutians and twenty-eight are new for Adak Island.

INTRODUCTION

Located in the Andreanof Group of the Aleutian Islands, Adak Island, Alaska, is about 45 km long and 35 km wide at its widest part. Volcanic in origin, the terrain is rugged and mountainous. Mount Moffett (approximately 1.2 km high), located on the northwest part of the island, is the highest peak on the island. Minor earthquakes are not unusual on Adak and there are several active volcanoes in the area (Coats, 1956; Fraser & Snyder, 1959). The island is completely treeless except for the "Adak National Forest," which consists of approximately 20 Sitka spruce trees (*Picea sitchensis*) planted by U.S. Navy personnel in 1951. Most of the island's vegetation is comprised of dwarf willows, herbaceous plants, grasses, mosses, and an abundance of wild flowers in the summer (Hein, 1976).

The numerous collections of vascular plants which have been made in the Aleutian Islands are cited by Hultén (1960) and Hein (1976). However, the reported lichen and bryophyte collections from the Aleutians are few (Merrill, 1929; Hedrick, 1936; Degelius, 1937; Bartram, 1938; Stair, 1948; Shacklette, 1966; Persson, 1968; Shacklette et al., 1969). Except for the small collection of lichens and mosses by Hultén in 1932 (Degelius, 1937; Bartram, 1938) and the cryptogam collection by Christian in 1946 and 1947 (Stair, 1948), there are no other known published reports of lichens or bryophytes from Adak Island. During a study of the island's vascular plants from 16 May through 26 September 1974 (Hein, 1976), a collection of lichens, liverworts, and mosses was made. Identifications were made by Dr. John Thomson, Department of Botany, University of Wisconsin-Madison (lichens) and Dr. William C. Steere of the New York Botanical Garden (liverworts and mosses). One set of lichens was deposited in the University of Wisconsin herbarium (WIS) and a set of liverworts and mosses was deposited in the herbarium of the New York Botanical Garden (NY). A partial replicate set of identified plants is in the Anderson Herbarium (ISC) at Iowa State University.

The annotated list of taxa following is arranged by families according to Hale & Culbertson (1966), Worley (1970), Crum, Steere, & Anderson (1973), and Stotler & Crandall-Stotler (1977).

DISCUSSION

Due to its cool, cloudy, and damp climate, Adak Island supports an abundant growth of lichens, liverworts, and mosses. On numerous vertical banks, such as the sides of foxholes or roadside cuts made during World War II, and along the edges of streams and lakes, the bryophyte growth is so luxuriant that it forms curtain-like overhangs and conical stalactite-like growths at water drip points such as were described for Amchitka Island, Alaska, by Shacklette et al. (1969). Of special interest in the lowlands and wider valleys on

¹Water and Air Research, Inc., P.O. Box 1121, Gainesville, Fl. 32602

Adak Island are distinctive conical moss mounds up to 1.5m high consisting mainly of *Sphagnum* moss. (Shacklette et al., 1969; Hein, 1976).

Since most of the collecting effort was directed toward the vascular plants of the island, this collection of lichens, liverworts, and mosses does not represent the total number of species which probably occurs on the island. Most of the taxa in the collection, however, have not been previously reported from Adak Island.

CHECK LIST

The numbers following names of taxa specify collection sites, which are listed at the end of the check list. Species marked * have not previously been reported from Adak Island; ** not previously reported from the Aleutians.

ASCOMYCETES (LICHENS)

Peltigeraceae

Peltigera apbthosa (L.) Willd. var *apbthosa* — 1. On rock surfaces.

**Peltigera horizontalis* (Huds.) Baumg. — 5. Hillside slopes.

**Peltigera malacea* (Ach.) Funck. — 4. Hillside slopes.

Cladoniaceae

**Cladonia amaurocraea* (Flörke) Schaer. — 1. Hillside slopes.

**Cladonia arbuscula* (Wallr.) Rabh. — 5. Hillside slopes.

**Cladonia coccifera* (L.) Willd. — 4. Hillside slopes.

**Cladonia lepidota* Nyl. probably f. *stricta* (Nyl.) Sandst. — 4. Hillside slopes.

***Cladonia pseudoevansii* Asah. — 5. Hillside slopes.

**Cladonia pyxidata* (L.) Hoffm. — 1. Hillside slopes.

Stereocaulaceae

***Stereocaulon botryosum* Ach. em Frey — 1. Hillside slopes.

**Stereocaulon tomentosum* Fr. — 5. Hillside slopes.

Umbilicariaceae

**Umbilicaria cylindrica* (L.) Del. in Duby — 1. On rock surfaces.

**Umbilicaria hyperborea* (Ach.) Hoffm. — 1. On rock surfaces.

Alectoriaceae

Alectoria ochroleuca (Hoffm.) Mass. — 4, 5. Hillside slopes and disturbed areas.

***Bryoria nitidula* (Th. Fr.) Brodo & Hawksw. — 5. Hillside slopes and disturbed areas.
Formerly known as *Alectoria nitidula* (Brodo & Hawksworth, 1977).

BRYOPHYTA: HEPATICAE (LIVERWORTS)

Adelanthaceae

***Odontoschisma macounii* (Aust.) Underw. — 5. Hillside slopes, sandy soil.

Lophocoleaceae

- **Chiloscyphus pallescens* (Ehrh. ex Hoffm.) Dum. — 6. Submerged in 0.3m of water.

Jungermanniaceae

- ***Jungermannia pumila* With. — 5. Hillside slopes, sandy soil.

Scapaniaceae

- **Scapania paludosa* (K. Müll.) K. Müll. — 5. Wet areas.

Pelliaceae

- ***Pellia epiphylla* (L.) Corda — 5. Wet areas.

Conocephalaceae

- **Conocephalum conicum* (L.) Lindb. — 5. Wet areas.

BRYOPHTA: MUSCI (MOSSES)

Sphagnaceae

- Sphagnum girgensohnii* Russ. — 5. Wet areas.

Dicranaceae

- **Dicranum majus* Turn. — 5. Wet areas.

Grimmiaceae

- Racomitrium canescens* var. *ericoides* (Hedw.) Hamp. — 5. Hillside slopes, sandy soil.

- Racomitrium fasciculare* (Hedw.) Brid. — 5. Hillside slopes, sandy soil.

- Racomitrium heterostichum* (Hedw.) Brid. — 4. Wet areas.

- Racomitrium lanuginosum* (Hedw.) Brid. — 5. Wet areas.

Splachnaceae

- **Tetraplodon mnioides* (Hedw.) B.S.G. — 4. Wet areas.

Bryaceae

- **Poblia nutans* (Hedw.) Lindb. — 5. Hillside slopes, sandy soil.

- Bryum pseudotriquetrum* (Hedw.) Schwaegr. — 5. Wet areas.

Mniaceae

- ***Mnium venustum* Mitt. — 3. Wet areas, sandy soil.

Bartramiaceae

- ***Philonotis caespitosa* Jur. — 5. Wet areas.

**Philonotis fontana* (Hedw.) Brid. — 4, 5. Wet areas.

Brachytheciaceae

***Homalothecium fulgescens* (C. Muell.) Jaeg. — 5. Wet areas.

**Brachythecium salebrosum* (Web. et Mohr) B.S.G. — 5. Wet areas.

Hylocomiaceae

Hylocomium splendens (Hedw.) B.S.G. — 5. Wet areas.

Polytrichaceae

**Polytrichastrum alpinum* Hedw. — 2, 5. Hillside slopes and wet areas.

COLLECTION SITES (number following name)

1. Area north of Heart Lake. Elevation 75m.
2. Bering Hill around enlisted Navy personnel barracks. Elevation 30m.
3. Bering Hill between enlisted Navy personnel barracks and galley. Elevation 30m.
4. East side of Lake Leone. Elevation 40-50m.
5. Hillside behind (W from) enlisted Navy personnel barracks. Elevation 30-75m.
6. Medium sized lake (ca. 60m. diam.) between enlisted Navy personnel barracks and White Alice station. Elevation 90m.

SUMMARY

This collection includes 37 species distributed among 24 genera and 21 families. Of 15 species of lichens, four have not been reported previously from the Aleutians and only two (*Alectoria ochroleuca* and *Peltigera aphthosa*) have been reported from Adak Island. None of the six species of liverworts collected have been reported from Adak and three of them are new for the Aleutians. Of the 16 species of mosses collected, three are new for the Aleutians and only seven have previously been reported from Adak Island.

ACKNOWLEDGEMENTS

I would like to express my sincere thanks to Dr. John Thompson of the University of Wisconsin-Madison and Dr. William C. Steere of the New York Botanical Garden for the definitive identification of my collections. I am also grateful to Dr. Richard W. Pohl and Mark L. Gabel of the Iowa State University herbarium for their assistance in the identification of my plants, for obtaining financial aid, and for access to the facilities of the Anderson herbarium during the time I was there.

I wish also to thank the personnel of Water and Air Research, Inc., for their financial support and assistance during the preparation of this manuscript.

LITERATURE CITED

- Bartram, E.B. 1938. Mosses of the Aleutian Islands, Alaska. Bot. Not. 1938: 244-256.
 Brodo, I.M. & D.L. Hawksworth. 1977. *Alectoria* and allied genera in North America. Opera Bot. 42: 1-164.
 Coats, R.R. 1956. Geology of northern Adak Island, Alaska. U.S. Geol. Surv. Bull. 1028-C: 45-67.

- Crum, H.A., W.C. Steere, & L.E. Anderson. 1973. A new list of mosses of North America north of Mexico. *Bryologist* 76: 85-130.
- Degelius, G. 1937. Lichens from southern Alaska and the Aleutian Islands, collected by Dr. E. Hultén. *Meddelanden Fran Göteborgs Bot. Trädg.* 12: 105-144.
- Fraser, G.D. & G.L. Snyder. 1959. Geology of southern Adak Island and Kagalaska Island, Alaska. U.S. Geol. Surv. Bull. 1028-M: 371-408.
- Hale, M.E., Jr., & W.L. Culberson. 1966. A third checklist of the lichens of the continental United States and Canada. *Bryologist* 69: 141-182.
- Hedrick, J. 1936. Lichens from the Aleutian Islands and the Alaska Peninsula. *Mich. Acad. of Sci., Arts, Letters Papers* 21: 75-80.
- Hein, M.K. 1976. Aspects of the flora of Adak Island, Alaska: Vascular plants. *Iowa State J. Res.* 51: 39-58.
- Hultén, E. 1960. Flora of the Aleutian Islands. Ed. 2. Hafner, New York, N.Y. 376 p.
- Merrill, G.K. 1929. A new list of Alaskan lichens in the genus *Cladonia*. *Bryologist* 32: 41-50.
- Persson, H. 1968. Bryophytes from the Aleutian Islands, Alaska, collected mainly by Hansford T. Shacklette. *Svensk Bot. Tidsk.* 62: 369-387.
- Shacklette, H.T. 1966. Unattached moss polsters on Amchitka Island, Alaska. *Bryologist* 69: 346-352.
- , *et al.* 1969. Vegetation of Amchitka Island, Aleutian Islands, Alaska. U.S. Geol. Surv. Prof. Paper 648. 66 p.
- Stair, L.D. 1948. A few cryptogams from Adak Island, Alaska. *Bryologist* 51: 247-248.
- Stotler, R. & B. Crandall-Stotler. 1977. A checklist of the liverworts and hornworts of North America. *Bryologist* 80: 405-428.
- Worley, I.A. 1970. A checklist of the Hepaticae of Alaska. *Bryologist* 73: 32-38.

IRRIGATION POTENTIAL ON IOWA SOILS OF HIGH WATER-HOLDING CAPACITY¹

D.C. Nielsen and R.H. Shaw²

ABSTRACT. A study of the irrigation potential of corn on Iowa soils of high water-holding capacity was conducted by using a soil-moisture computer model with simulated irrigation for nine locations in Iowa. A weighted stress index was calculated and used in a regression equation to estimate corn yields.

Two levels of irrigation management were compared in July–September irrigations: one initiated when only 25% of the available moisture in the root zone was depleted and the other starting when 50% had been depleted. The two levels of irrigation management showed little difference in yield response.

Yield increases due to irrigation were largest in northwestern Iowa and least in eastern and southeastern Iowa. On the basis of the 1958-1977 period, average yield increases per year due to irrigation ranged from 416 kg/ha in eastern and southeastern Iowa to 3250 kg/ha in northwestern Iowa. For these same areas, yield increases for individual years ranged from 0 to 2550 kg/ha and 52 to 9680 kg/ha.

In years with low spring soil moisture, the effect of preseason irrigation and summer irrigation was compared with summer irrigation only. The average yield increase due to preseason irrigation was only 19 kg/ha.

INTRODUCTION

Moisture stress arises when soil-moisture reserves and precipitation fail to supply the amounts of moisture required by plants. Severe moisture stress occurs only occasionally in Iowa but can greatly reduce corn yields. Short periods of mild moisture stress are of more common occurrence across most of the state. Mild stress during midday over a period of time can measurably reduce yields.

This paper reports work done with a computer simulation model to study the effects of soil moisture and moisture stress on corn. Climatological data were used in the model to determine the potential for irrigation on Iowa soils of high water-holding capacity.

LITERATURE REVIEW

The amount of water needed by a growing corn crop has been reported by Rhoades and Nelson (1955), Denmead and Shaw (1959), Schleusener and Kruse (1963), Downey (1971), and Shaw (1977). Most values fall in the range of 40 to 64 cm during the growing season, although amounts from 30 to 84 cm have been reported. The wide range in values is partly due to different periods of growth studied. Factors causing increased growth, such as frequent irrigations, increased plant populations, and increased fertilization tend to increase the consumptive use of water by corn (Rhoades and Nelson, 1955; Power et al., 1973), but once high population levels and high fertility have been reached, added amounts increase water use only slightly.

¹Journal Paper No. J-9660 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa, Project 1852.

²Graduate Research Assistant and Professor of Agricultural Climatology, Department of Agronomy, Iowa State University, Ames, Iowa 50011.

Shaw et al. (1958) estimated water lost from land in corn in Iowa from evapotranspiration, runoff, and percolation. Normal precipitation from April 15 to October 31 was 60 cm, while the average use for the same period was 63.8 cm. Average use was greater than, or equal to, normal monthly precipitation in late June, July, and August. Presumably the average seasonal deficit of 3.8 cm could easily be made up from normal soil-moisture reserves. Average, or "normal," conditions, however, seldom occur, and a corn crop may run short of moisture for short periods during the growing season. Later, excess rains may provide a positive seasonal water balance, even though moisture-stress damage had occurred. Yield loss is dependent on the time of occurrence and severity of the stress.

Moisture stress decreases corn yield by interrupting photosynthesis and checking growth until turgor is restored. Yields also are limited by moisture stress at the sensitive silking stage, which causes the timing of silk emergence and pollen-shed to be disrupted and may result in barren plants. Estimates of yield reductions due to moisture stress range from 3% to 11% per day of stress (Robins and Domingo, 1953; Denmead and Shaw, 1960; Claussen and Shaw, 1970), and thus small amounts of moisture stress at critical time periods will reduce yields. Colville et al. (1964) and Beer et al. (1967) concluded that even though corn had either ample rainfall or sufficient irrigations to maintain soil-moisture reserves at a high level, yields were reduced by temporary moisture-stress periods due to high atmospheric demand.

In Iowa, Beer et al. (1967), on the basis of six years data at Ames, reported a net yield increase for irrigated corn over nonirrigated corn. The response to irrigation usually was greater at higher rates of nitrogen fertilization and at higher plant populations. Schwab et al. (1958), reporting on work done near Conesville and Ankeny, Iowa, from 1951 to 1955 found that yield responses at both locations varied from year to year because of differences in environmental conditions, but generally, that irrigation increased yields. Such increases were greater at higher stand and fertility levels. The authors concluded that some increase in corn yields can be expected on most well-drained soils in most years in Iowa.

BACKGROUND INFORMATION AND PROCEDURES

Nine sites (Figure 1) were chosen for evaluation of irrigation effects on corn yields in Iowa, these representing the nine Iowa crop-reporting districts, exclusive of the south-central district, which was eliminated to minimize computation costs. Soil moisture and meteorological conditions in this district were similar to those in southeastern Iowa. Descriptions of these sites have been provided by Nielsen (1979). The soil types have been described by Oschwald et al. (1965).

Initial (spring) soil-moisture amounts and field-capacity values by 15.2-cm intervals down to 152 and 213 cm, date of 75% silking, daily pan-evaporation data, and daily rainfall amounts from these nine sites over a period from 1958 to 1977 were used in the soil-moisture computer program described by Dale and Hartley (1963) and modified by Morris (1972). This program was used in the present study. An 85-day, weighted, moisture-stress index (Shaw, 1974) also was calculated. This index (X) is used to estimate corn grain yields (Y , kg/ha) in the regression equation:

$$Y = 9682 - 118.6X$$

as given by Shaw (1978).

The application of 2.54 cm of effective plant-available water every three days (if required) with a large-center-pivot, sprinkler irrigation system, was simulated by a FORTRAN subroutine incorporated into the soil-moisture program. Irrigation was used as needed from July 1 (calendar date) through September 30 (date adjusted to silking). This procedure neglected the possible occurrence of dry spring weather. However, since



Figure 1. Location of test sites.

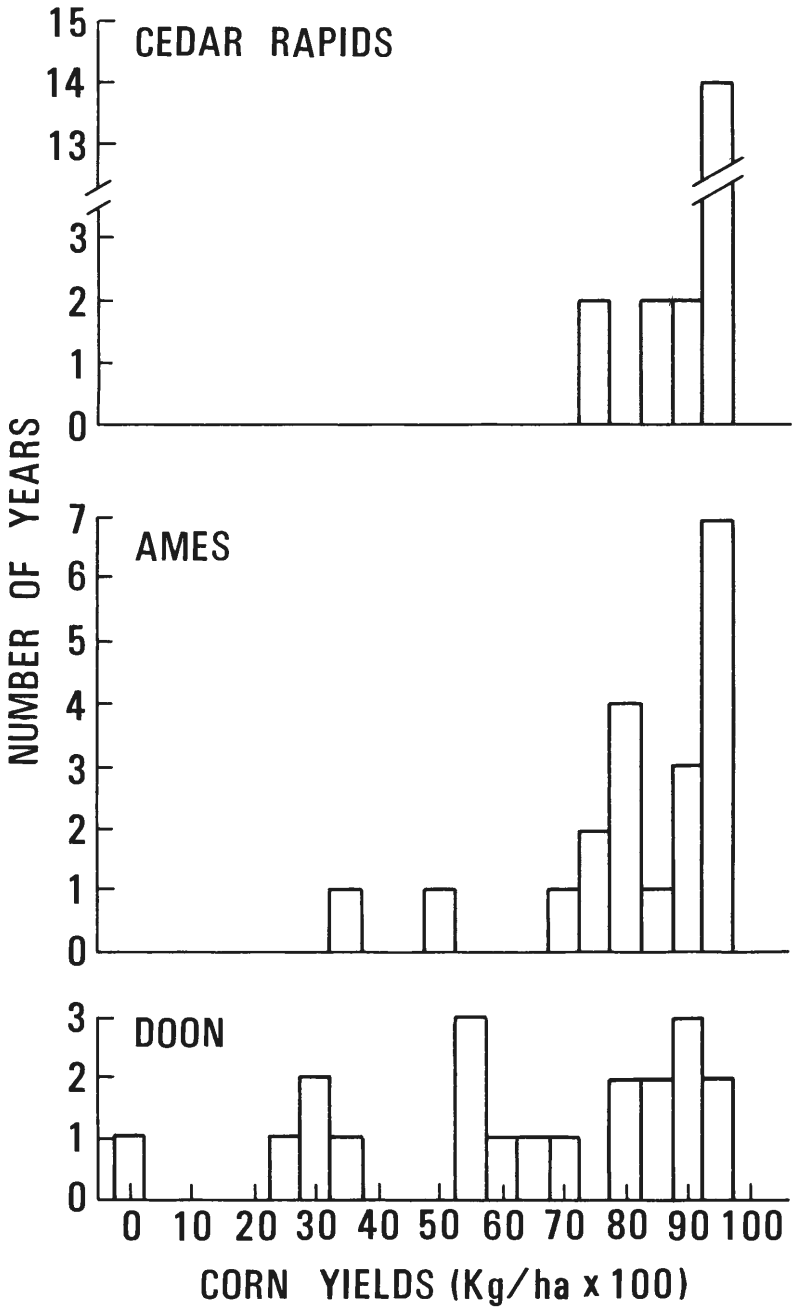


Figure 2. Frequency distributions of calculated unirrigated corn yields for Doon, Ames, and Cedar Rapids, 1958–1977.

June irrigation may cause excess-moisture problems if subsequent rains fill the profile and because the effect of this variable could not be evaluated, it was decided to start irrigation on July 1.

Two methods, based on field capacity criteria, were used. One method, a high level of irrigation management, specified irrigation when the available soil moisture in the active root zone (Shaw, 1963) was reduced to 75% of field capacity. Under the second procedure, irrigation was supplied when the available moisture in the active root zone was reduced to 50% of field capacity. In both management systems, irrigation, when supplied, was continued until the available moisture in the active root zone was brought up to within 2.54 cm of 90% of the field capacity value. Yields of unirrigated and irrigated corn and corn-yield increases for each station for each year of data were then calculated. Also, the amount of irrigation water applied per season for each of the two scheduling criteria at each of the nine stations was calculated.

Irrigation in humid and subhumid regions can increase the occurrence of excess moisture problems, which may reduce yields. To roughly evaluate this problem, three-month (July, August, and September) percolation sums were calculated for each year for the unirrigated and the two irrigated situations, and percolation was calculated (Shaw, 1963). Percolation is defined as the water that drains from the bottom of the soil profile after all layers above have been brought to field capacity. Percolation amounts indicate a possible harvesting problem due to wetness. A year was considered to have a potential wetness problem if the three-month percolation total was greater than or equal to 2.54 cm and if 80% or more of the three-month total occurred in September.

Yield data for 1958-1977 without irrigation for the nine stations used in this study were used as a base from which to determine the effects of irrigation.

RESULTS AND DISCUSSION

Frequency distributions of calculated unirrigated corn yields for the Northeast Research Center (Doon), Agronomy and Agricultural Engineering Research Center (Ames), and Cedar Rapids are given in Figure 2. The distribution for Doon is representative of the distributions for extreme northwestern Iowa, the driest part of the state. It shows that yields were reduced moderately by moisture stress in several years and reduced severely by moisture stress in some other years. The distribution for Cedar Rapids is representative of the distributions for eastern and southeastern Iowa. Generally, yields were only slightly reduced by moisture stress, but moderate yield reductions occurred in a couple of years. The distributions for north-central and central Iowa, intermediate to those for Doon and Cedar Rapids, were similar to the distribution given for Ames, usually being more evenly split between the high yields and the moderately reduced yields. Yields were, however, severely reduced in a few years.

Table 1 shows the averages and ranges of expected yield increases due to irrigation as computed with the irrigation subroutine. Average yield increases were greatest in northwestern Iowa, averaging 3250 kg/ha at Doon and 2200 kg/ha at Sutherland. Increases in individual years ranged from 59 to 9680 at Doon and 29 to 6820 at Sutherland. In western Iowa (Castana) the average yield increase was 1720 kg/ha with a range of 10–6510. In eastern and southeastern Iowa, the average yield increase was 416 kg/ha with a range from 0 to 2550. Average yield increases in northern, central and southwestern Iowa were between those for west-central and eastern Iowa.

The amount of irrigation water applied per irrigation season was influenced by the amount of soil moisture available to the plant, the amount of rainfall during the growing season, and the atmospheric evaporative capacity. As expected, the amount of irrigation water applied varied greatly from year to year. In general, the applied amounts with the 75% criterion were greatest in northwestern Iowa (ave. 26.7 cm) and least in eastern (11.7 cm) and southeastern Iowa (12.7 cm). The averages and ranges of seasonal applica-

Table 1. Yield increases due to irrigation (kg/ha), 1958-1977.

Station	Average Increase	Range of Increase
Northwest Research Center (Doon)	3250	52-9680
Northwest Research Center (Sutherland)	2200	29-6820
Agronomy and Agricultural Engineering Research Center (Ames)	1310	6-4740
Burlington-Columbus Junction	417	0-2550
Western Research Center (Castana)	1720	10-6510
Cedar Rapids	416	0-2250
Elkader	704	0-3420
Northern Research Center (Kanawha)	1040	0-3860
Norwich-Shenandoah	1360	0-4220

Table 2. Average (and range) of seasonal irrigation application amounts, in cm.

Station	50% Criterion	75% Criterion
Northwest Research Center (Doon)	24.5 (10.2-48.3)	26.7 (10.2-48.3)
Northwest Research Center (Sutherland)	19.2 (0.0-40.6)	24.4 (7.6-45.7)
Agronomy and Agricultural Engineering Research Center (Ames)	13.6 (0.0-38.1)	17.9 (5.1-38.1)
Burlington-Columbus Junction	9.4 (0.0-27.9)	12.7 (0.0-25.4)
Western Research Center (Castana)	17.4 (2.5-48.3)	19.9 (7.6-48.3)
Cedar Rapids	7.7 (0.0-20.3)	11.7 (2.5-22.9)
Elkader	10.8 (0.0-33.0)	14.1 (0.0-33.0)
Northern Research Center (Kanawha)	13.0 (0.0-33.0)	17.0 (5.1-40.6)
Norwich-Shenandoah	14.1 (0.0-33.0)	18.0 (2.3-33.0)

tion amounts of irrigation water, Table 2, show that more water was applied with the 75% criterion than with the 50% criterion. Although this difference was statistically significant only at Cedar Rapids, the trend is evident, since in all but one of the 180 site-years studied, the amount of irrigation water applied with the 75% criterion was equal to or greater than the amount applied with the 50% criterion.

There was no statistical difference between the yields obtained when using the 50% scheduling criterion or the 75% scheduling criterion for irrigation. Irrigation seemed equally effective in reducing moisture stress for all areas of the state.

With the 75% criterion, irrigation was used in 99% of the site-years. When the 50% criterion was applied, irrigation was necessary in only 81% of the site-years. This is a substantial reduction in the proportion of years requiring irrigation and constitutes a practical argument for scheduling irrigation by the latter criterion, especially as conservation of water, energy, and labor are becoming more important concerns.

The results of the evaluation of a possible excess-moisture problem showed that the potential was greatest in eastern and southeastern Iowa and least in northwestern Iowa, and that irrigation increased the likelihood of the problem. These conclusions are based on the assumption that a more highly charged soil-moisture profile is more likely to become saturated if the normal pattern of precipitation in the fall occurs, but no calculations were made to quantify the effect.

The data show that, in some years, some moisture stress, mostly of two distinct kinds, was not eliminated by the regular season irrigation:

1. Moisture stress that occurred preceding the initiation of irrigation on July 1. This condition occurred in 29% of the years studied. The average pre-July stress (averaged only over years when pre-July stress occurred) was 1.50 stress units, causing a yield reduction of 178 kg/ha. (One unit of stress reduces yield 118.6 kg/ha). The range of pre-July stress values was 0.05 to 11.22 units.

2. Moisture stress that occurred after July 1. This moisture stress occurred in dry years when irrigation water could not be put on sufficiently rapidly; i.e. in such years, the addition of water at the rate of 2.54 cm/3 days did not suffice to meet the high atmospheric demand and at the same time recharge the depleted soil-moisture profile.

Both kinds of moisture stress could be ameliorated by the initiation of irrigation before July 1. But a conflict might then develop between early irrigation and some cultivation operations. Perhaps a better method for removing this stress would be with pre-season irrigation.

The effects of preseason irrigation on early stress were evaluated in a simple, approximate manner by adjusting the initial soil-moisture profile to 80% of field capacity. In a farming situation, this might be equivalent to application of water in the fall after harvest or early in the spring before planting. In years with very dry spring conditions (initial soil-moisture profile less than 40% of field capacity for Ames, Burlington-Columbus Junction, Cedar Rapids, Elkader, and Kanawha; less than 70% for Doon, Sutherland, Castana, and Norwich-Shenandoah), preseason irrigation was simulated followed by regular-season irrigation after June 30 scheduled by the 50% criterion.

Preseason irrigation affected the 85-day weighted-stress index, seasonal percolation total, amount of seasonal irrigation water applied, timing of irrigation, and the times at which stress occurred. Although changes in these quantities generally were not statistically significant, certain trends were evident for the three western stations (Doon, Sutherland, and Castana) where the 70% of field capacity criterion for picking years for preseason irrigation gave a larger sample size than for the other stations used. For these three stations, preseason irrigation tended to decrease slightly the 85-day weighted-stress index, increase the average seasonal percolation total, and decrease the amount of regular-season irrigation, which began on or after July 1. No consistent shift in the timing of irrigation could be seen. The greatest yield increase was 576 kg/ha, but it was normally 50 kg/ha or less. The average yield increase for all years in which preseason irrigation was used at

these three sites was only 19 kg/ha. Little benefit, compared with regular-season irrigation, was obtained on the high moisture-capacity soils.

In many years when preseason irrigation was specified by the criteria used, the actual growing-season rainfall and summer irrigation were adequate to remove stress. This was because of good spring rains following the preseason irrigation. The potential for excess wetness in the spring could not be evaluated with the model tested here. On the other hand, some moisture stress which did not qualify for preseason irrigation occurred during five years. Low rainfall and high atmospheric evaporative capacity were such that the moisture in the root zone was depleted to a stress condition, and preseason irrigation or irrigation before July 1 would have been beneficial. Until we have an accurate forecast for "next summer's" weather, these problems with irrigation scheduling cannot be avoided.

SUMMARY AND CONCLUSIONS

A study of the irrigation potential of corn on soils of high water-holding capacity in Iowa was conducted by computer simulation. A computer model that used spring soil moisture, daily rainfall, and daily pan-evaporation data to estimate the moisture balance of a growing corn crop was used to determine a weighted, seasonal moisture-stress index. This weighted-stress index was used in a regression equation to estimate corn yields.

The effects of irrigation by a large, center pivot, sprinkler irrigation system were simulated by incorporating into the soil-moisture program a subroutine which, on call, added 2.54 cm of plant-available irrigation water to the soil profile every three days until the cut-off point was reached. Nine stations were chosen to determine the differential effects of irrigation across the state. Soil moisture, rainfall, and pan-evaporation data for 1958-1977 were used in the computer simulation.

Two methods for scheduling irrigation were tested. One method represented a high level of irrigation management and called for irrigation when only 25% of the available moisture had been used. The other method represented a lower level of irrigation management and called for irrigation when 50% of the available moisture had been used. There was no yield advantage associated with the higher level of irrigation management.

Corn yields were reduced by moisture stress to some degree almost every year at most Iowa locations, although in many years, the reductions were small. These reductions in yield were greatest in northwestern Iowa and least in eastern and southeastern Iowa. When irrigation was used, yield reductions due to moisture stress were minimal. Increased yield due to irrigation was greatest in northwestern Iowa where average yield increases of 3250 kg/ha were predicted. In eastern and southeastern Iowa, the smallest increase was predicted, averaging only 416 kg/ha.

The amount of water applied was greatest in northwestern Iowa and least in eastern and southeastern Iowa. Generally more water was needed under the higher level of irrigation management. The frequency of a potential fall-wetness problem was greatest in eastern and southeastern Iowa and least in northwestern Iowa and was increased when irrigation was used.

The effects of preseason irrigation were roughly evaluated and it was generally concluded that, for stations in western and northwestern Iowa (where preseason irrigation could be used more frequently than in other areas of the state), preseason irrigation plus regular season irrigation, compared with regular season irrigation, tended to decrease slightly the 85-day weighted-stress index, increase the average seasonal-percolation total, and decrease the amount of irrigation water applied during the season. The average yield increase, compared with regular-season irrigation, was only 19 kg/ha.

From the results of this study, it can be concluded that irrigation can be used to reduce moisture stress and raise corn yields to some degree almost every year at most Iowa locations on soils of high water-holding capacity. However, the greatest potential

for increasing corn yields with irrigation is in northwestern Iowa. Other areas of the state could benefit to some degree from irrigation in many years, but this benefit is not as great and does not occur as often as in northwestern and western Iowa. The economic aspects of this type of irrigation program were not investigated in this study.

LITERATURE CITED

- Beer, C.E., W.D. Schrader, and R.K. Schwanke. 1967. Interrelationships of plant population, soil moisture and soil fertility in determining corn yields on Colo clay loam at Ames, Iowa. Iowa Agric. Home Econ. Exper. Sta. Res. Bull. 556.
- Claussen, M.M., and R.H. Shaw. 1970. Water deficit effects on corn. II. Grain components. *Agron. J.* 62: 652-655.
- Colville, W.L., A Dreier, D.P. McGill, P. Grabouski, and P. Ehlers. 1964. Influence of plant population, hybrid and "productivity level" on irrigated corn production. *Agron. J.* 56: 332-335.
- Dale, R.F., and M. Hartley. 1963. Computer program for estimating soil moisture under corn (Multilithed appendix to final report to U.S. Weather Bureau on Contract CWB-10544). *Agron. Dept., Iowa State University, Ames.*
- Denmead, O.T., and R.H. Shaw. 1959. Evapotranspiration in relation to the development of the corn crop. *Agron. J.* 51: 725-726.
- and -----, 1960. The effects of soil moisture stress at different stages of growth on the development and yield of corn. *Agron. J.* 52: 272-274.
- Downey, L.A. 1971. Water requirements of maize. *J. Austral. Instit. Agric. Sci.* 11: 32-41.
- Morris, R.A. 1972. Simulation-model-derived weather indexes for regressing Iowa corn yields on soil, management and climatic factors. Ph.D. Dissertation, Iowa State University, Ames.
- Nielsen, D.C. 1979. Computer simulation of the irrigation potential of corn on high water-holding capacity soils in Iowa. M.S. Thesis, Iowa State University, Ames.
- Oschwald, W.R., F.F. Reicken, R.I. Didericksen, W.H. Scholtes, and F.W. Schaller. 1965. Principal soils of Iowa: their formation and properties. Iowa Ext. Serv. Special Report 42.
- Power, J.F., J.J. Bond, W.A. Sellner, and H.M. Olson. 1973. Effect of supplemental water on barley and corn production in a subhumid region. *Agron. J.* 65: 464-467.
- Rhoades, H.F., and L.B. Nelson. 1955. Growing 100-bushel corn with irrigation. USDA Yearbook of Agriculture, U.S. Govn. Print. Off., Washington, D.C.
- Robins, J.S., and C.E. Domingo. 1953. Some effects of severe soil moisture deficits at specific growth stages of corn. *Agron. J.* 45: 618-621.
- Schleusener, P.E., and E.G. Kruse. 1963. Empirical formula for computing the water needs of a row crop. *Trans. Amer. Soc. of Agric. Eng.* 6: 140-141, 144.
- Schwab, G.O., W.D. Schrader, P.R. Nixon, and R.H. Shaw. 1958. Research on irrigation of corn and soybeans at Conesville and Ankeny, Iowa, 1951-1955. Iowa Agric. Home Econ. Exp. Sta. Res. Bull. 458.
- Shaw, R.H. 1963. Estimation of soil moisture under corn. Iowa Agric. Home Econ. Exp. Sta. Res. Bull. 520.
- , 1974. A weighted moisture-stress index for corn in Iowa. *Iowa State J. Res.* 49: 101-114.
- , 1977. Climatic requirement. In: G.F. Sprague (ed.). Corn and corn improvement. Agronomy Monograph 18: 591-623. American Society of Agronomy, Madison.
- , 1978. Calculation of soil moisture and stress conditions in 1976 and 1977. *Iowa State J. Res.* 53: 119-127.

- , J.R. Runkles, and G.L. Barger. 1958. Seasonal changes in soil moisture as related to rainfall, soil type and crop growth. Iowa Agric. Home Econ. Exp. Sta. Res. Bull. 457.

RELATIONSHIPS OF PREVIOUS SPORT PARTICIPATION, AGE, AND SEX
WITH EXPRESSED ATTITUDES TOWARD SPORT TEAM PARTICIPATION

Dale G. Pease and Dean F. Anderson¹

ABSTRACT. We studied the feelings and attitudes of children about participation in team sports by administering a questionnaire to 240 fifth and sixth grade students from a rural Iowa community. The study examined the associations between the independent variables of previous team sport participation, sex and age with the dependent attitudinal variables concerning sport team participation, winning and rewards. Results indicate that playing on a sport team was felt to be important regardless of sex, age or previous participation. There was little association between children's previous sport participation and the dependent variables studied. Importance of playing on a winning team, importance of close contests and importance of rewards were found to be associated with age. Only the importance of playing on a winning team was found to be associated with a child's sex.

INTRODUCTION

It is estimated that more than 20 million youngsters participate every year in youth league sport programs sponsored by schools and other community organizations. Every year the number of participants increases but, as the number of participants increases, so does criticism of the programs. Many people question the immediate and long term physical, psychological, and sociological effects "Little Leaguism" has upon young participants.

Much of the limited psychological and sociological research on youth sports programs has been concerned with participants attitudes toward play. One attitudinal concept, "professionalization," designates a decreasing importance given to fair play while the importance of displaying skill and winning increases. Webb's (1969) data concerning children's professionalized attitudes toward play show significant changes from grade three to grade twelve, the greater changes being for male children. Studies by Mantel and Vander Velden (1974), Maloney and Petrie (1972), and McAfee (1955) report an association between sport participation and professionalized attitude toward play. This evidence seems to suggest that age, sex and type of sport involvement may be important factors relating to children's attitudes toward sport team participation.

It has been suggested that the structure of little league programs where adults play a role may be an important factor in the development of attitudes children display toward sport team participation (Coakley, 1978; Devereux, 1976; Orlick and Botterill, 1975). In spontaneous play situations children control almost every aspect of the activity including the rule making, officiating and rewarding. However, in the little league game, parents, managers and officials share in the play process. Most of the current research involving attitudes has been done with intact teams such as little league baseball (Roberts, 1978; Watson, 1976), soccer (Scanlan and Passer, 1978) and hockey (Tyler and Duthrie, 1979). Because of sample limitation, it has been difficult to see whether the changes observed in children's attitudes toward sport participation are due to participation in organized youth sport programs or are merely part of the common social, psychological development process. Therefore, the object of this investigation was examination of the associations between the independent variables of previous sports participation, sex and age

¹Department of Physical Education, Iowa State University, Ames, Iowa.

with the dependent attitudinal variables concerning sport team participation, winning and rewards.

PROCEDURE

A rural community in central Iowa, population approximately 6500, was used as the site for this research. The community selected has a comprehensive, all seasons, adult organized sport programs for children. All members of the grades sampled received letters requesting parental permission to participate in this study. Three parents, accounting for five children, refused permission to allow their children to take part, and eleven students chose not to respond to the questionnaire. All remaining fifth and sixth grade students ($n = 240$) in the school district were given the three page questionnaire during their regular physical education class time. The students were told about the purpose of the project and helped through the demographic selection of the questionnaire, i.e. that concerning age, sex and past participation on organized sport teams. They were then asked to continue through the questionnaire, seeking help only from the experimenter. Few questions were asked.

The questionnaire was developed to investigate the importance of participation on sport teams and the importance of different aspects of sport team participation such as winning, skill development and the importance of rewards such as trophies, uniforms and travel. To establish the content validity of the items, experts from Child Development, Physical Education, and Sociology reviewed the questionnaire. Language of the instrument was pretested by children of the same age as those in the sample, in order to help insure that subjects would understand the terms used.

RESULTS

Seventy-three percent of the male subjects and fifty percent of the female subjects participated in at least one team sport program sponsored by non-school organizations.² Of all children, sixty-one percent were participants, the greatest proportion, seventy percent, being among 12 and 13 year old children.

Data indicate that playing on a sport team is important to the elementary school children investigated. Results presented in Table 1 show that over fifty percent of the children sampled felt it was very important to play on a sport team. Another forty percent responded that it was "somewhat important." As could be expected, children who had experience participating in organized sport programs outside the school system more frequently responded "very important." Even though these results are statistically significant, data show that playing on a sport team is "very important" or "somewhat important" for eighty-five percent or more of the children sampled regardless of previous sport experiences. No statistically significant results were found for the independent variables of sex and age.

Playing on a winning sport team is not as important as being a member of a sports team. Only twenty-one percent of the children felt that it was "very important" to play on a winning sport team as compared to the fifty-four percent which felt it was "very important" to play on a sport team. No statistically significant differences were found between participants and nonparticipants in the frequency of responses concerning the importance of playing on a winning sports team. However, significant age and sex differences were found for the importance of playing on a winning sport team. Results in Table 2 show that forty-five percent of the ten year olds, and seventy-five percent of

²These are the participants in subsequent terminology; those who did not take part in sports are non-participants.

TABLE 1

Participant and nonparticipant differences for the importance of playing on a sport team.

	Participant	Nonparticipant	Total
	(Percent)	(Percent)	(Percent)
Very important	60.3	44.0	54.0
Somewhat important	37.0	44.0	39.7
Weakly important	2.1	7.7	4.2
Not important	0.7	4.4	2.1
Totals	100.1 (n=146)	100.1 (n=91)	100.0 (n=237)*
Chi square = 11.33		p = 0.010	

* Three children, one participant, and two nonparticipants did not respond to this question.

TABLE 2

Age differences for the importance placed upon playing on a winning sport team.

	AGE			Totals
	10	11	12/13	
	(Percent)	(Percent)	(Percent)	(Percent)
Very important	8.3	21.6	28.8	21.1
Somewhat important	37.5	32.6	46.6	38.0
Weakly important	22.9	11.2	12.3	13.9
Not important	31.3	34.5	12.3	27.0
Totals	100.0 (n=48)	100.0 (n=116)	100.0 (n=73)	100.0 (n=237)*
Chi square = 20.09		p = 0.003		

* Three children, one from each age group, did not respond to this question.

twelve and thirteen year olds responded "very important" or "somewhat important." These data indicate that almost twenty-five percent more of the twelve and thirteen year old children than the ten and eleven year old children felt that playing on a winning sport team was "very or somewhat important." Data presented in Table 3 show that sixty-seven percent of the male children responded "very important" or "somewhat important" as compared to fifty percent of the female children. Participation on a winning sport team seems to be important more frequently for older children than for younger children and important more frequently for male children than female children.

TABLE 3

Sex differences for the importance placed upon playing on a winning sport team.

Sex	Male	Female	Totals
	(Percent)	(Percent)	(Percent)
Very important	20.4	21.8	21.1
Somewhat important	46.9	29.8	38.0
Weakly important	9.7	17.7	13.9
Not important	23.0	30.6	27.0
Totals	100.0 (n=113)	100.0 (n=124)	100.0 (n=237)*
Chi square = 8.589		p = 0.035	

* Three children, two males and one female, did not respond to this question.

Playing on a sport team which receives rewards such as trophies and travel is not as important to children investigated as playing on sport teams and playing on winning sport teams. Only fifty percent of the children responding felt that it was "very important" or "somewhat important" to play on a sport team which received such extrinsic rewards. No sex association or participation association was found for the importance of playing on a sport team which receives extrinsic rewards such as trophies and travel. Although the results in Table 4 show statistical significance, the age data are not interpretable. Data in the "very important" response category show a slight increase in frequency as age increases. However, if the two top categories are combined, there is a U-shaped distribution for response frequency.

Besides the presence of trophies and travel in the adult organized sport teams, uniforms are frequently provided by the adults for the young participants. Results concerning importance of playing on a team with nice uniforms display statistically significant associations for participation and age. Even though significant associations are shown, playing on a sport team with nice uniforms is not of major importance among the children studied. Only twenty-three percent of the children felt it was "very important" or "somewhat important." These data are presented in Tables 5 and 6. Table 6 shows that the frequency of "very important" and "somewhat important" responses increases about ten percent each year. Nice uniforms were more frequently regarded as important by the nonparticipants.

TABLE 4

Age differences for the importance of playing on a sport team which receives rewards.

	10	11	AGE 12/13	Totals
	(Percent)	(Percent)	(Percent)	(Percent)
Very important	12.8	17.4	21.6	17.8
Somewhat important	46.8	24.3	33.8	31.8
Weakly important	23.4	26.1	32.4	27.5
Not important	17.0	32.2	12.2	22.9
Totals	100.0 (n=47)	100.0 (n=115)	100.0 (n=74)	100.0 (n=236)*
Chi square = 16.503			p = 0.011	

* Four children, two 10 year olds and two 11 year olds, did not respond to this question.

TABLE 5

Participant and nonparticipant differences in the importance of playing on a sport team that has nice uniforms.

	Participants	Nonparticipants	Total
	(Percent)	(Percent)	(Percent)
Very important	2.7	8.7	5.0
Somewhat important	13.7	23.9	17.6
Weakly important	20.5	20.7	20.6
Not important	63.0	46.7	56.7
Totals	99.9 (n=146)	100.0 (n=92)	99.9 (n=238)*
Chi square = 9.94		p = 0.020	

* Two children, one participant and one nonparticipant, did not respond to this question.

TABLE 6

Age differences in the importance of playing on a sport team that has nice uniforms.

	AGE			Totals
	10	11	12/13	
	(Percent)	(Percent)	(Percent)	(Percent)
Very important	6.3	3.4	6.8	5.0
Somewhat important	4.2	18.1	25.7	17.6
Weakly important	22.9	29.0	21.6	20.6
Not important	66.7	59.9	45.9	56.7
Totals	100.0 (n=48)	100.0 (n=116)	100.0 (n=74)	100.0 (n=238)*
Chi square = 11.63			p = 0.011	

* Two children, one 10 year old and one 11 year old, did not respond to this question.

TABLE 7

Age differences in the importance of close contests when playing on a sport team.

	AGE			Totals
	10	11	12/13	
	(Percent)	(Percent)	(Percent)	(Percent)
Very important	39.6	59.5	62.2	56.3
Somewhat important	31.3	22.4	29.7	26.5
Weakly important	14.6	6.9	5.4	8.0
Not important	14.6	11.2	2.7	9.2
Totals	100.0 (n=48)	100.0 (n=116)	100.0 (n=74)	100.0 (n=238)*
Chi square = 13.276			p = 0.039	

* Two children, one 10 year old and one 11 year old, did not respond to this question.

It is important that the sport contest be close. Over eighty percent of the children responding felt that close contests were "very important" and "somewhat important." A statistically significant age association is displayed in Table 7. Once again, the frequency of "very important" and "somewhat important" responses increases approximately ten percent each year. No significant participation and sex difference were obtained.

DISCUSSION AND CONCLUSIONS

When interpreting the results presented here, one must remember that the data were limited to a sample of fifth and sixth grade children from one rural community in Iowa and might differ under other cultural conditions. Results obtained indicated that playing on a sport team was felt to be important. This view, expressed by these elementary school children, may be similar to the results found for high school students. Results of Buhrman and Bratton (1977), Coleman (1961), and Eitzen (1976) have repeatedly shown the importance of athletic prowess as a criterion for high status in the adolescent subculture. Thus, it is possible that colleges socialize high schools which socialize junior high schools, and so on down to the elementary grades. The influence on the lower grades has been observed as early as 1925 (Lynd and Lynd, 1929, p. 212).

The relative lack of significant associations between the children's previous sport participation and dependent variables studied suggest that the impact of adult intervention in the organized sport situation has been minimal. Specifically, results concerning importance of winning, importance of playing on a sport team that receives rewards and the importance of close contests when playing on a sport team failed to show statistically significant differences between participants in organized team sport programs and nonparticipants. However, the idea of the importance of playing on a team with nice uniforms was of greater import for nonparticipants than participants. One possible explanation for the relative lack of significant associations between participants and nonparticipants may be that the very nature of sport activities resists the impact of adult intervention. Also, it is possible that the method used to differentiate participants and nonparticipants in this study was incapable of resolving differences.

Significant age associations for the importance of playing on a winning sport team and for close contests supports Webb's (1969) report. His investigation of children stratified by grades (3, 6, 8, 10, and 12) clearly showed an increasing importance of winning in the play situation as age increased. The importance of playing on a sports team that has nice uniforms also increased with age. The number and direction of the significant age associations suggest the influence of the adolescent subculture and can be compared to the research of Buhrmann and Bratton (1977), Coleman (1961) and Eitzen (1976).

Significant sex differences found for the importance placed upon winning are similar also to those reported by Webb (1969). The greater emphasis upon victory by males than females would seem to be consistent with differential experiences both groups may have acquired with respect to ascriptive and achievement criteria for status. However, the lack of any other statistically significant sex associations in the data suggest that cultural patterns concerning sport participation may be changing.

LITERATURE CITED

- Buhrmann, H.G. and R.D. Bratton. 1977. Athletic participation and status of Alberta high school girls. *Intern. Rev. Sport Sociology*. 12: 57-67.
- Coakley, J. 1978. Sport for youngsters: wholesome fun or ritualized boredom? In: *Sport and Society: Issues and Controversies*. C.V. Mosby, St. Louis.
- Coleman, J.S. 1961. *The adolescent society: the social life of the teenager and its impact on education*. Free Press, New York.
- Devereux, E. 1976. Backyard versus Little League baseball: the impoverishment of chil-

- dren's games. In: Landers, D. (ed.). *Social problems in athletes*. Univ. Ill. Press, Urbana.
- Eitzen, D.S. 1976. Athletics in the status system of male adolescents. A replication of Coleman's the adolescent society. In: Yiannakis, A. (ed.). *Sport sociology: Contemporary themes*. Kendall/Hunt, Dubuque.
- Lynd, R. and H. Lynd. 1929. Middletown. Harcourt, Brace and Brace, New York.
- Maloney, T.L. and B.M. Petrie. 1972. Professionalization of attitude toward play among Canadian school pupils as a function of sex, grade, and athletic participation. *J. Leisure Res.* 4: 184-195.
- Mantel, R.C. and L. Vander Velden. 1974. The relationship between the professionalization of attitude toward play of pre-adolescent boys and participation in organized sport. In: Sage, G.H. (ed.). *Sport and American society*. Addison-Wesley, Reading.
- McAffee, R.A. 1955. Sportsmanship attitude of sixth, seventh and eighth grade boys. *Amer. Assoc. Health, Phys. Ed. Recreation Res. Quart.* 26: 26.
- Orlick, T. and C. Botterill. 1975. *Every kid can win*. Nelson-Hill, Chicago.
- Roberts, G. 1978. Children's assignment of responsibility for winning and losing. In: Smoll, F. and R. Smith (eds.). *Psychological perspectives in youth sports*. John Wiley, New York.
- Scanlan, T. and M. Passer. 1978. Anxiety-inducing factors in competitive youth sports. In: Smoll, F. and R. Smith (eds.). *Psychological perspectives in youth sports*. John Wiley, New York.
- Tyler, J. and J. Duthie. 1979. The effect of ice hockey on social development. *J. Sport Behav.* 2: 49-59.
- Watson, G. 1976. Reward systems in children's games: the attraction of game interaction in Little League baseball. *Rev. Sport Leisure.* 1: 93-121.
- Webb, H. 1969. Professionalization of attitudes toward play among adolescents. In: Keyon, G. (ed.). *Aspects of contemporary sport sociology*. Athletic Institute, Chicago.

HATCHABILITY OF EGGS AND MATING SUCCESS OF EUROPEAN CORN BORER CULTURES REARED CONTINUOUSLY ON A MERIDIC DIET^{1, 2}

F.A. Onukogu³, W.D. Guthrie⁴, W.H. Awadallah⁵, and J.C. Robbins⁶

ABSTRACT. On the basis of spermatophore counts, mating in European corn borer, *Ostrinia nubilalis* (Hübner), cultures M133 and M160 (reared for 133 and 160 generations on a meridic diet) was about the same as in the check culture. Corn borer cultures CI.31AF, CI.31AL, Oh43F, Oh43L, WF9F, and WF9L (reared for one generation each year on corn plants in the field and eight generations on a meridic diet) mated as many or more times than did the check culture.

Hatchability of eggs, incubated at 27°C or 16°C and high humidity, for M133 and M160 was less than was hatchability of eggs from the check cultures in three experiments. In two other tests, however, hatchability of eggs (incubated at 28°C and high humidity) was relatively high in all cultures, whereas hatchability of eggs incubated at 28°C and low humidity was low in all cultures. Thus it was not demonstrated that low hatchability contributed to low survival in the field.

Deficient mouth parts evidently do not contribute to low survival of corn borer cultures M133 and M160 on corn plants under field conditions; several hundred larvae of these two cultures were compared with a check culture (M5) and all apparently had normal mouth parts.

INTRODUCTION

As reported by Guthrie et al. (in press), European corn borer, *Ostrinia nubilalis* (Hübner), cultures M160 and M133 have been reared on a meridic diet (contains one or more chemically undefined ingredients) for 160 and 133 generations, respectively. Corn borer cultures CI.31AF, Oh43F, and WF9F have been reared for 13 generations on corn and 104 generations on a meridic diet (one generation each year on corn and eight generations on a meridic diet). Corn borer cultures CI.31AL, Oh43L, and WF9L have been reared 11 generations on corn and 108 generations on a meridic diet (one generation each year on corn and eight generations on a meridic diet from 1965 through June 1976 and 11 generations each year on a meridic diet from July 1976 through 1978). Large egg masses were selected for advancing each corn borer culture to the next generation. M160 and M133 have lost their ability to survive on corn plants in the field (Guthrie et al., 1971).

¹Lepidoptera: Pyralidae.

²Joint contribution: Corn Insects Research Unit, Agricultural Research, Science and Education Administration, USDA, and Journal Paper No. 9579 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa 50011. Project No. 2183.

³Graduate student, Iowa State University, Ames, Iowa 50011.

⁴Research Entomologist, Corn Insects Research Unit, Agricultural Research, Science and Education Administration, Ankeny, Iowa 50021, and Professor, Department of Entomology, Iowa State University, Ames, Iowa 50011.

⁵Visiting scientist, Ministry of Agriculture, Cairo, Egypt.

⁶Agricultural Research Technician, Corn Insects Research, Agricultural Research, Science and Education Administration, USDA, Ankeny, Iowa 50021.

In 1978, we conducted several experiments to determine behavioral changes of European corn borer cultures reared continuously on a meridic diet. This research is part of an ongoing series of studies to determine the most effective method of maintaining insects in the laboratory without changing characteristics important in research.

One objective of our research was to determine mating frequencies in these corn borer cultures. Fye and LaBrecque (1966) reported that males of three races of flies, *Musca domestica* (L), reared for many generations in the laboratory were less acceptable to females than were the males of natural populations. Prokopy et al. (1972) reported that laboratory caged apple maggots, *Rhagoletis pomonella* (Walsh), were unable to mate or oviposit seven-eight days after emergence, indicating that there are mating behavioral changes in laboratory insects.

Our second objective was to determine if different temperatures and humidity affect hatchability of egg masses from corn borer cultures reared continuously on a meridic diet. The cultures have been reared for many generations under 27-28°C and 75-90% RH.

Our third objective was to determine if corn borer cultures M160 and M133, which have lost their ability to survive on corn plants in the field, have deformed mouth parts. Knipling (1960) has postulated that it might be possible to develop deficiencies in immature stages of insects which would lead to their destruction. Deformed mouth parts in larvae is a deficiency that might interfere with development of an insect in nature, though not affect their survival in the laboratory.

METHODS AND MATERIALS

In experiments I through V, virgin female and male moths of eight cultures of corn borers (M160, M133, CI.31AF, CI.31AL, Oh43F, Oh43L, WF9F, and WF9L) and a culture used as a check (reared on a meridic diet for five generations, M5) were placed in oviposition cages. The oviposition room was operated at 27°C during 18 hr each day and 16-20°C during six hr each day. The cycling temperature was required to insure adequate mating, as reported by Guthrie et al. (1971).

In experiment I, the mating frequencies of corn borers reared continuously on a meridic diet was determined. A randomized block design with six replications was used (100 females, 115 males/cage/corn borer culture = 11,610 moths for the nine cultures). The moths were allowed to mate in the cages for six days. Female moths were then killed and preserved in 75% alcohol; female moths were dissected, and the number of spermatophores in each female of each corn borer culture was determined; spermatophores are an index of the number of times that female moths mate (Showers et al., 1974).

In experiments II, III, IV, and V, effect of temperature and humidity on the hatchability of egg masses from corn borer cultures reared continuously on a meridic diet was determined. The method of egg production was reported by Guthrie et al. (1971). Female moths oviposited on sheets of waxed paper placed on top of each cage (two sheets of 15 cm x 60 cm/cage). The criteria used for evaluating hatchability of egg masses for the nine corn borer cultures were: (1) percentage of eggs that hatched, (2) percentage of eggs that embryonated without hatching, and (3) percentage of sterile eggs. The size of eggs masses was also determined in experiment II.

In experiment II, the waxed paper containing egg masses was replaced with new papers daily for nine-ten days. A total of 5,400 female moths was used; these moths would be expected to produce ca. 54,000 egg masses (ca. 1,350,000 eggs); a 10% sample of egg masses on each sheet of waxed paper (taken at random) was used. Disks of waxed paper containing one egg mass/disk were cut out each day and pinned onto celotex boards; these boards were wrapped in moist paper, placed in plastic bags, and incubated at 27°C for four days. At the blackhead stage of embryonic development, the boards with egg masses were spread out to allow the hatching larvae to crawl away. The egg masses (after hatching) were observed under a compound light microscope. A total of 2,781 egg masses

(56,050 eggs) were examined.

In experiment III, egg masses from female moths used in experiment II were utilized. A randomized block design with four replications was used. Each replication contained 50 egg masses of each of the nine corn borer cultures for a total of 200 egg masses/culture. Disks of waxed paper containing one egg mass/disk were cut out and pinned onto celotex boards (50 masses/board). The egg masses were handled the same as experiment II; 1,800 masses (38,813 eggs) were examined.

Experiment IV was also based on egg masses derived from experiment II. The procedure was identical with that of experiment III except that the egg masses (on celotex boards) from the nine corn borer cultures were incubated at a temperature of 16°C and ca. 95% RH instead of 27°C. In 10-12 days (blackhead stage of embryonic development) the boards were spread out in a room operating at 27°C and 75-80% RH to allow the hatching larvae to crawl away; 1,800 egg masses (39,580 eggs) were examined.

In experiment V, virgin moths of nine corn borer cultures were placed into oviposition cages (200 pairs of moths/cage, one cage/culture). Egg masses for these studies were from the fourth day of moth oviposition. Disks of waxed paper containing one egg mass/disk were cut out and pinned onto celotex boards (25 egg masses/board). A randomized block design with four replications (25 egg masses/replication) was used for each of three levels of humidity which were:

(1) Ca. 100% RH until all eggs had hatched; the boards containing egg masses were wrapped in moist paper, placed in plastic bags, and incubated at 27°C (27,224 eggs were examined.)

(2) Ca. 100% RH for four days (blackhead stage of embryonic development) and one day at 35% RH. The boards containing the egg masses were wrapped in moist paper, placed in a plastic bag, and incubated at 27°C for four days; the egg masses were then removed from the plastic bag, unwrapped, and exposed to 27°C and 35% RH (23,279 eggs were examined).

(3) Ca. 35% RH until all eggs had hatched; the boards containing egg masses were incubated at 27°C and 35% RH (33,209 eggs were examined).

In experiment VI, differences in mouth parts of corn borers reared continuously on a meridic diet were sought. Corn borer cultures M160, M133, and M5 (check) were individually reared on plugs of diet in three-dram vials (one larva/vial). A randomized block design with six replications was used (51 larvae/replication/instar of each culture). A total of 306 second-instar larvae, 306 third-instar larvae, and 306 fifth-instar larvae of each culture was placed in KAAD for 24 hr, preserved in 75% alcohol, and examined with a compound light microscope for deficient mouth parts, particularly differences in the mandibles.

RESULTS

Experiment I

The analysis of variance showed significant differences between corn borer cultures in mating frequencies on the basis of spermatophore counts (Table 1). Corn borer cultures M5, M160, M133, Oh43F, and WF9L mated a maximum of four times; CI.31AL and Oh43L mated a maximum of five times; and CI.31AF and WF9F mated a maximum of six times. Mean spermatophore counts for the nine cultures ranged from 1.2 to 2.1 spermatophores/female moth. Corn borer cultures M133 and M160 had about the same number of spermatophores as did the check culture (M5). Cultures CI.31AF, CI.31AL, Oh43L, and WF9F had the greatest number of spermatophores. In general, cultures reared continuously on a meridic diet in the laboratory (M133, M160) mated as many times as did a check culture, whereas most of the corn borer cultures reared one generation each year on corn in the field and eight generations each year on a meridic diet in the laboratory (CI.31AF, CI.31AL, Oh43L, and WF9F) mated more times than did the check culture.

Table 1. Mating frequencies of European corn borer cultures reared continuously on a meridic diet (Experiment I).

Cultures	Percentage of females with 0 to 6 spermatophores							Mean ¹
	0	1	2	3	4	5	6	
M5	20.7	48.0	22.0	8.7	0.6	0.0	0.0	1.2
M160	16.0	33.3	36.7	13.3	0.7	0.0	0.0	1.5
M133	23.3	46.0	20.7	8.0	2.0	0.0	0.0	1.2
CI.31AF	2.7	29.3	36.0	24.7	5.3	1.3	0.7	2.1
CI.31AL	2.7	25.7	38.0	26.3	4.0	3.3	0.0	2.0
Oh43F	16.0	40.7	33.3	8.7	1.3	0.0	0.0	1.4
Oh43L	6.7	24.4	39.3	26.3	2.7	0.6	0.0	1.9
WF9F	5.3	27.3	40.7	22.7	2.0	0.7	1.3	1.9
WF9L	24.0	42.0	24.0	9.3	0.7	0.0	0.0	1.2

¹LSD.05 any two means between cultures = 0.45.

Experiment II

The number of eggs/mass ranged from 13.3 for corn borer culture Oh43L to 19.4 for culture CI.31AF (Table 2). Egg masses of corn borer cultures M133 and M160 contained the same number of eggs as those of the check culture (M5) and did not differ significantly from most of the other cultures.

Hatchability of eggs for corn borer cultures M133 (reared for 133 generations on a meridic diet containing wheat germ) and M160 (reared for 160 generations on a diet containing dried-ground corn leaves) was significantly less than was hatchability of eggs from the check culture and was significantly less than was hatchability of most of the cultures reared one generation each year on corn in the field and eight generations each year on a meridic diet in the laboratory (CI.31AF, CI.31AL, Oh43F, Oh43L, WF9F, and WF9L).

Experiment III

The data in Table 3 show that hatchability of eggs for corn borer culture M160, incubated at 27°C and high humidity, was significantly less than was hatchability of eggs for the check cultures (M5), i.e. 58.6% vs 76.4%, and was significantly less than the hatchability of eggs for most of the cultures reared for one generation each year on corn in the field and eight generations each year on a meridic diet in the laboratory (CI.31AF, CI.31AL, Oh43F, Oh43L, and WF9L). No significant differences were detected between hatchability of eggs for corn borer culture M133 and the check culture or corn borer culture M160.

Table 2. Number of eggs/mass and hatchability of European corn borer egg masses incubated at 27-28°C and high humidity (Experiment II).

Cultures	Number of eggs counted	Number eggs/mass ¹	Range in number eggs/mass	Percent hatched ¹	Percent embryonated without hatching ¹	Percent sterile ¹
M5	5,852	16.3b	3-59	74.2a	13.0ab	12.8cd
M160	6,228	16.1b	2-78	64.5b	11.3abcd	24.2a
M133	5,500	16.3b	2-69	66.9b	13.8a	19.3ab
CI.31AF	4,428	19.4a	3-56	76.9a	12.4abc	10.6d
CI.31AL	5,197	18.3ab	1-72	67.3b	10.6bcd	22.1ab
Oh43F	4,685	17.6ab	1-53	78.0a	9.9cde	12.1cd
Oh43L	4,015	13.3c	2-53	74.5a	7.5e	18.0bc
WF9F	5,106	17.7ab	3-71	73.9a	8.5de	17.6bc
WF9L	5,039	17.6ab	1-66	75.3a	11.9abc	12.9cd

¹Means within a column followed by the same letter do not differ significantly at 5% level of probability (Duncan's multiple range test).

Table 3. Hatchability of European corn borer egg masses incubated at 27°C and 16°C and high humidity (Experiments III and IV).

Cultures	Percent hatched ¹		Percent embryonated without hatching ¹		Percent sterile ¹	
	27°C	16°C	27°C	16°C	27°C	16°C
M5	76.4a	73.4a	5.7a	8.7c	17.4abc	17.8b
M160	58.6b	50.2b	10.5a	12.5ab	31.8a	37.3a
M133	68.3ab	67.2a	8.3a	12.8a	27.3ab	20.0b
CI.31AF	77.2a	67.7a	8.6a	10.7abc	15.5abc	21.6b
CI.31AL	78.6a	61.8ab	8.8a	8.2c	12.1bc	30.0ab
Oh43F	76.2a	74.4a	9.5a	8.9bc	5.8c	16.7b
Oh43L	80.5a	70.7a	8.9a	11.1abc	10.0bc	18.2b
WF9F	74.4ab	77.2a	9.8a	10.2abc	13.1bc	12.7b
WF9L	82.8a	69.5a	9.6a	11.0abc	5.0c	19.5b

¹Means within each column followed by the same letter do not differ significantly at 5% level of probability (Duncan's multiple range test).

Table 4. Hatchability of European corn borer egg masses incubated at 27°C and RH of 100% until egg hatch (columns 1,4,7); RH of 100% until blackhead stage of embryonic development and at 35% RH until egg hatch (columns 2,5,8); and RH of 35% until egg hatch (columns 3, 6,9). Experiment V.

	Percent hatched ¹			Percent embryonated without hatching ¹			Percent sterile ¹		
	27°C	27°C	27°C	27°C	27°C	27°C	27°C	27°C	27°C
Cultures	100% RH	100-35% RH	35% RH	100% RH	100-35% RH	35% RH	100% RH	100-35%RH	35% RH
M5	88.8ab	77.5ab	19.7c	9.5abc	18.9ab	73.2a	1.7a	3.6a	7.1b
M160	85.9b	72.1b	20.9c	14.0a	23.8a	67.6abc	0.1a	4.1a	11.5a
M133	90.0ab	77.3ab	28.9abc	8.4bc	18.6ab	63.3bcd	1.6a	4.1a	7.8ab
Cl.31AF	85.1b	73.7ab	25.1bc	11.9ab	19.5ab	65.4abc	3.0a	6.8a	9.6ab
Cl.31AL	95.0a	84.9a	31.8ab	4.6c	11.0b	60.1bcd	0.4a	4.1a	8.1ab
Oh43F	91.7ab	83.1ab	37.8a	7.1bc	11.9b	54.7bcd	1.2a	5.0a	7.5ab
Oh43L	89.2ab	78.8ab	28.9abc	9.4abc	14.6ab	65.5abc	1.4a	6.6a	8.0ab
WF9F	84.9b	75.5ab	25.0bc	12.1ab	20.1ab	69.7ab	3.0a	4.4a	5.3b
WF9L	88.5ab	73.2b	25.1bc	9.2abc	23.0a	65.9abc	2.3a	3.8a	9.0ab

¹Means within each column followed by the same letter do not differ significantly at 5% level of probability (Duncan's multiple range test).

Experiment IV

The data in Table 3 show that hatchability of eggs for corn borer culture M160, incubated at 16°C and high humidity, was significantly lower than hatchability of eggs of the check culture (M5) i.e., 50.2% vs 73.4%. Hatchability of eggs for M160 was also significantly lower than hatchability of eggs of a culture (M133) reared for 133 generations on a meridic diet containing wheat germ and of most of the cultures reared one generation each year on corn in the field and eight generations each year on a meridic diet in the laboratory (CI.31AF, Oh43F, Oh43L, WF9F, and WF9L).

Experiment V

Hatchability of eggs of all corn borer cultures was high when incubated under high-humidity conditions. The range was 84.9% for corn borer culture WF9F to 95.0% for corn borer culture CI.31AL (Table 4). Hatchability of eggs for corn borer cultures M133 and M160 (reared on a meridic diet in the laboratory for 133 and 160 generations, respectively) was not significantly different from that of the check culture (M5), and was not significantly different from that of most of the cultures reared each year for one generation on corn plants in the field and eight generations each year on a meridic diet in the laboratory (CI.31AF, CI.31AL, Oh43F, Oh43L, WF9F, and WF9L).

Hatchability of eggs for all corn borer cultures was relatively high when incubated under high humidity conditions until the blackhead stage of embryonic development (ca. four days) and 35% RH until completion of hatching (ca. one day). The range, in this instance, was 72.1% for corn borer culture M160 to 84.9% for corn borer culture CI.31AL (Table 4). Hatchability of eggs for M133 and M160 was not statistically different from that of the check culture (M5) and was not significantly different from that of most of the other corn borer cultures.

Hatchability of eggs of corn borer culture M160 was determined in 1967 in the 49th generation of larval rearing on a meridic diet; 78.4% of the eggs hatched, 13.6% of the eggs embryonated without hatching, and 8% of the eggs were sterile (unreplicated test; 47,128 eggs from 148 female moths examined). The eggs were incubated under high humidity conditions until the blackhead stage of embryonic development (ca. four days) and at 35% RH until all eggs had hatched (ca. one day).

Hatchability of eggs for all corn borer cultures was low when continuously incubated under low (35% RH) humidity conditions (Table 4). The range in egg hatchability was 19.7% for corn borer culture M5 to 37.8% for corn borer culture Oh43F. Hatchability of eggs for M133 and M160 was not significantly different from that of the check culture (M5) and was not significantly different from that of most of the other corn borer cultures.

Experiment VI

We did not observe deficient mouth parts in any larvae of corn borer cultures M160, M133, and M5.

SUMMARY AND DISCUSSION

Spermatophore counts suggested that the mating frequencies of corn borer cultures reared continuously on a meridic diet for 133 or 160 generations were about the same as that of a check culture. Corn borer cultures reared one generation on corn in the field and eight generations each year on a meridic diet mated as many or more times as did the check culture.

In general, data from experiments II, III, and IV suggest a deterioration of hatch-

ability of eggs from a corn borer culture reared for 160 generations (M160) on a meridic diet containing dried-ground corn leaves. Data from Experiment V, however, show that hatchability of eggs from M160 approached that of eggs from the check culture (M5). Hatchability of eggs from a culture reared for 133 generations (M133) on a meridic diet containing wheat germ was numerically greater, but usually not significantly different than that from culture M160. Because the survival inconsistencies of these cultures as compared with the check, we are not certain whether hatchability of their eggs contributes to low larval survival in the field.

Hatchability of eggs from corn borer cultures reared for one generation each year on corn in the field and eight generations each year on a meridic diet in the laboratory (CI.31AF, CI.31AL, Oh43F, Oh43L, WF9F, and WF9L) was as great or greater than was hatchability of eggs from the check culture in all tests.

Since larvae of corn borer cultures M133 and M160 had normal mouth parts, a structural deficiency seemingly does not contribute to low field survival. Since these cultures have been reared many generations under near optimum conditions of temperature and humidity, without natural selection for outdoor fluctuating temperatures and low humidity, possibly their field failure is physiologically based.

LITERATURE CITED

- Fye, R.L., and C.C. LaBrecque. 1966. Sexual acceptability of laboratory strains of male house flies in competition with wild strains. *J. Econ. Ent.* 59: 538-540.
- Guthrie, W.D., F.A. Onukogu, W.H. Awadallah, J.C. Robbins, and M.L. Lodholz. Changes in survival and development of cultures of European corn borers reared in the laboratory on a meridic diet. *Iowa State J. Res.* (In press).
- , W.A. Russell, and C.W. Jennings. 1971. Resistance of maize to second-brood European corn borers. *Proc. Ann. Corn-Sorghum Res. Conf.* 26: 65-79.
- Knipling, E.F. 1960. Use of insects for their own destruction. *J. Econ. Ent.* 53: 415-420.
- Prokopy, R.J., E.W. Bennet, and G.L. Bush. 1972. Mating behavior of *Rbagoletis pomonella* (Diptera: Tephritidae). *Can. Ent.* 104: 97-104.
- Showers, W.B., G.L. Reed, and H. Oloumi-Sadeghi. 1974. Mating studies of female European corn borers: Relationship between deposition of egg masses on corn and captures in light traps. *J. Econ. Ent.* 67: 616-619.

BEHAVIOR AND SURVIVAL OF CULTURES OF EUROPEAN CORN
BORERS REARED ON A MERIDIC DIET IN DISHES^{1,2}

W.D. Guthrie³, F.A. Onukogu⁴, W.H. Awadallah⁵, and J.C. Robbins⁶

ABSTRACT. Larval survival among cultures of European corn borers, *Ostrinia nubilalis* (Hübner), differing in multiple generation treatment-history, were compared. Larvae were reared on synthetic diet and survival recorded on the basis of number pupating. Fewer larvae of two cultures reared for 133 and 160 generations on synthetic diet in the laboratory survived to pupation than did those of the check or of six cultures which were reared one generation each year on corn in the field and eight generations on diet in the laboratory. Seemingly, an annual one generation intercalation on corn in the field favors survival of culture progeny. Fewer larvae of culture M160 crawled out of the diet into corrugated strips of paper to pupate than did any other culture.

INTRODUCTION

This paper is part of an ongoing series of tests to determine the most effective method of maintaining insects in the laboratory without changing characteristics important in research. Techniques for maintaining usable cultures should be available should natural populations decline with the consequence that new cultures cannot be started each year.

Millions of egg masses of European corn borers, *Ostrinia nubilalis* (Hübner), reared in the laboratory are used each season for artificial infestation of corn plants (Guthrie et al., 1971). For large scale production of egg masses, larvae are now reared in plastic dishes (25.4 cm diam and 8.9 cm deep) containing 930 g of synthetic diet.

Our study was designed to determine whether corn borer larvae reared for many generations on diet plugs in 3-dr vials would survive if they were exposed to crowded conditions in dishes and whether such larvae would crawl out of the diet into strips of corrugated paper to pupate.

MATERIALS AND METHODS

Eight corn borer cultures (M160, M133, CI.31AF, CI.31AL, Oh43F, Oh43L, WF9F, and WF9L) have been maintained at the Corn Insects Research Unit for many generations. The history of these cultures is currently reported by Guthrie et al. (1980). Corn borer cultures M160 (reared on a meridic diet for 160 generations) and M133 (reared on a

¹Lepidoptera: Pyralidae.

²Joint contribution: United States Department of Agriculture, Science and Education Administration, Agricultural Research, and Journal Paper No. J-9577 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa 50011.

³Research Entomologist, Corn Insects Research Unit, Agricultural Research, Science and Education Administration, USDA, Ankeny, Iowa 50021, and Professor, Department of Entomology, Iowa State University, Ames, Iowa 50011.

⁴Graduate student, Iowa State University, Ames, Iowa 50011.

⁵Visiting scientist, Ministry of Agriculture, Cairo, Egypt.

⁶Agricultural research technician, Corn Insects Research Unit, Agricultural Research, Science and Education Administration, USDA, Ankeny, Iowa 50021.

meridic diet for 133 generations) were reared for successive generations on plugs of diet in three-dr vials (one larva/vial, 500 larvae/generation for M160; two larvae/vial, 500 larvae/generation for M133). Cultures CI.31AF, Oh43F, and WF9F were reared for 13 generations on corn in the field and 104 generations on a meridic diet (one generation each year on corn and eight generations each year on a meridic diet from 1965 through 1978). Corn borer cultures CI.31AL, Oh43L, and WF9L were reared for 11 generations on corn and 108 generations on a meridic diet (one generation each year on corn and eight generations each year on a meridic diet from 1965 through June, 1976; and 11 generations each year on a meridic diet from July, 1976 through 1978).

Those cultures which were annually rotated to corn were reared in the laboratory from 1965–1976 on plugs of diet in three-dr vials (two larvae/vial, 500 larvae/generation) and from 1977–1978 on diet in dishes (930 g of diet/dish, infested with ca. 1000 eggs). Culture M5 (check) was reared for two generations on plugs of diet in three-dr vials and for three generations on diet in dishes.

European corn borer larvae reared continuously on a meridic diet cannot be used in evaluating corn genotypes for resistance factors because leaf feeding damage is too low to permit measuring differential resistance (Guthrie et al., 1971).

In the present study, each dish was infested with 40 blackhead egg masses (ca. 1000 eggs). An effort was made to place the same size egg masses of each culture on diet in the dishes, but the actual number of eggs per dish was not determined. The dishes, therefore, probably did not receive the same number of eggs.

Two dishes of each of the nine cultures were started daily over a period of ten days for a total of 20 dishes/corn borer culture (1000 egg masses/dish = ca. 20,000 eggs/culture). Each dish constituted one replication in a randomized block design. Strips of corrugated paper (2.5 cm wide, treated in hot wax) were placed in the dishes as described by Guthrie et al. (1971). The incubation room was maintained at 27–28°C and a RH of 75% with constant light. Twenty-one days after egg hatch, the corrugated strips containing pupae were placed in oviposition cages and maintained at the same conditions. After all moths had emerged from the strips, pupal cases were counted.

Some larvae remained in the dishes to pupate; the number was recorded.

RESULTS AND DISCUSSION

The analysis of variance showed significant differences between corn borer cultures in larval survival and in percentage larvae crawling out of the diet into the strips of corrugated paper. Fewer larvae of corn borer culture M160 crawled out of the diet into corrugated strips to pupate than did any other culture including the check (Table 1). Thus, the behavior of culture M160 has changed in this respect. Approximately the same percentage of larvae of M133 and larvae of the check culture crawled out of the diet into corrugated strips to pupate. The remaining six cultures all had a higher percentage of pupation in the strips than the foregoing three.

Survival of corn borer larvae in cultures M160 and M133 was lower than in M5 and the other six cultures (Table 1). Hatchability of egg masses of M160 and M133 was as high as the check culture in some experiments, but was lower in other experiments (Onukogu et al., 1980). M160 and M133 reared on diet plugs in vials, one or two larvae/vial, had over 93% survival to pupation (Guthrie et al., 1980).

Finally, the fact that M160 and M133 were infected to some extent with *Nosema pyrausta* Paillot, may have had an effect on the survival of these two cultures. This microsporidian, however, did not affect the survival of M160 and M133 in several other experiments (Guthrie et al., 1980; Onukogu et al., 1980). The numbers of larvae surviving (Table 1) are not conclusive but do suggest that corn borers from cultures reared for at least 133 generations on plugs on diet in three-dr vials (one or two larvae/vial) do not

Table 1. Survival of European corn borer larvae on a meridic diet in dishes and percentage of larvae that crawled into strips of corrugated paper to pupate vs. percentage that pupated in dishes.

Cultures	Percentage of larvae in		Total no. surviving	
	Dish	Strip	Per dish	Per 20 dishes
M5 (check)	27.6	72.4	753.5	15,069
M160	35.7	64.3	610.6	12,211
M133	28.0	72.0	639.0	12,780
CI.31AF	17.9	82.1	948.7	18,974
CI.31AL	20.6	79.4	861.2	17,223
Oh43F	16.6	83.4	891.2	17,823
Oh43L	17.1	82.9	902.9	18,057
WF9F	16.0	84.0	899.9	17,997
WF9L	17.7	82.3	834.5	16,690
LSD 0.05	3.1		69.5	

survive as well in crowded dishes as do larvae from cultures reared one generation each year on corn in the field and eight generations each year on a meridic diet in dishes.

LITERATURE CITED

Guthrie, W.D., W.A. Russell, and C.W. Jennings. 1971. Resistance of maize to second-brood European corn borers. *Proc. Ann. Corn-Sorghum Res. Conf.* 26: 65-79.

-----, F.A. Onokogu, W.H. Awadallah, J.C. Robbins, and M.L. Lodholz. Changes in survival and development of cultures of European corn borers reared in the laboratory on a meridic diet. *Iowa State J. Res.* (In press).

Onokogu, F.A. W.D. Guthrie, W.H. Awadallah, and J.C. Robbins. Mating success and hatchability of eggs of European corn borer cultures reared continuously on a meridic diet. *Iowa State J. Res.* 54: 347-355.

EFFECT OF INSECTICIDE APPLICATIONS ON INSECT PREDATORS
OF THE EUROPEAN CORN BORER IN CENTRAL IOWA^{1,2}

C.R. Edwards, E.C. Berry, and T.A. Brindley³

ABSTRACT. Granular and spray formulations of carbofuran, DDT, diazinon, and EPN applied to small plots were compared to determine their effect on potential insect predators of the European corn borer, *Ostrinia nubilalis* (Hübner), in central Iowa. Over the entire sampling period, none of the insecticides significantly reduced *Orius insidiosus* (Say) adult populations. In early planted corn, *O. insidiosus* nymphs were significantly reduced over the entire sampling period by all granular formulations. In late planted corn, spray formulations produced the greatest reduction in populations. The combined data for coccinellid adults showed that only carbofuran spray in late planted corn significantly reduced the population in 1971. Numerically, however, all insecticides other than carbofuran granules substantially lowered the overall population. Coccinellid larval populations showed little reduction due to spray or granular formulations.

INTRODUCTION

Hill (1945) found that dust and spray formulations of DDT significantly reduced populations of *Orius insidiosus* (Say), coccinellids, and *Nabis* spp, and that DDT had little effect on *Chrysopa* spp. In contrast, Ripper (1956) reported complete elimination of *Chrysopa* with DDT. In addition, he reported highly toxic effects of EPN on *Coleomegilla maculata* (DeGeer) and *Hippodamia convergens* Guerin-Meneville, as well as for *Nabis ferus* (L.). Johansen and Eves (1967) reported that carbofuran applied in granular formulation as a sidedress and broadcast by airplane on alfalfa was relatively nontoxic to *Orius* spp., *H. convergens*, *Chrysopa*, and *Nabis alternatus* Parshley.

MATERIALS AND METHODS

Four chemicals that either at one time had been approved and recommended for control of the European corn borer, *Ostrinia nubilalis* (Hübner), or had proven to be effec-

¹Joint contribution: Agricultural Research, Science and Education Administration, USDA, and Journal Paper No. J-9113 of the Iowa Agriculture and Home Economics Experiment Station, Ames. Project No. 2183. A thesis submitted by the first author in partial fulfillment of the requirements of the Ph.D. degree.

²Mention of a pesticide in this paper does not constitute a recommendation for use by the USDA nor does it imply registration under FIFRA as amended. Mention of a proprietary product in this paper does not constitute an endorsement of this product by the USDA or its cooperators.

³Respectively: Former graduate student, Iowa State University, Ames. Presently Associate Professor, Department of Entomology, Purdue University, West Lafayette, Indiana 47907; Research Entomologist, Agricultural Research, Science and Education Administration, USDA, Corn Insects Research Unit, Ankeny, Iowa 50021; and Research Entomologist, Agricultural Research, Science and Education Administration, USDA, Corn Insects Research Unit, and Professor, Department of Entomology, Iowa State University, Ames, Iowa 50011. Presently retired.

tive were evaluated. These chemicals were carbofuran, DDT, diazinon, and EPN. Two applications of each chemical were applied as a spray and a granular formulation ca two weeks apart after the 1st and 3rd artificial infestation of corn borers. DDT and diazinon were applied at 1.12 kg AI/ha, while EPN and carbofuran were applied at 0.56 kg AI/ha.

Plots were arranged in a randomized complete block design replicated four times. Each plot was 27.4 m long by 12 rows wide with the four center rows treated with insecticides. A corn-borer-susceptible doublecross corn, (WF9 x LF5) x (GN2BD1 x IDT), was used. Seed was planted on 76.2 cm centers on May 21, 1970, and May 5, 1971, for early planting tests, and on May 29, 1970, and June 2, 1971, for late planting tests.

The middle 15 m of the six center rows of each plot were thinned to ca one plant every 30.5 cm to facilitate sampling. Every other plant was designated as a potential sample and was given a random identification number. The plants located between the potential samples were designated as guard plants to assure continued presence of plants throughout the season in all sample areas.

To assure that a borer population would be present for attracting predators, each plant in the four center rows of each plot was infested with one blackheading corn borer egg mass (ca 25 eggs). Plots were infested to coincide with natural borer oviposition.

The plots were sampled between 0100 and 0400 every two to four days, weather permitting, from June 17 to August 26, 1970, and from June 14 to August 20, 1971. This time had been determined to be best for recovery of above-ground insect predators by observations and evaluations of plant samples taken over a 24-h period at the beginning of the season.

The sampling technique used by McFarland (1963) was modified to facilitate the handling of large numbers of samples. In our study the designated plant was located and the bag was swiftly placed over the plant. The bag was quickly gathered tightly around the base of the stalk, which was in turn cut and pushed into the bag. The opened end of the bag was then tightly twisted and taped to prevent the escape of the arthropods.

Two samples were taken from the center of each plot, one each for either rows 1 and 3 or rows 2 and 4. Plots were sampled in this skip-row manner to insure as little disturbance as possible to the other row when the 1st sample was being taken. All samples were then placed in a 4°C cooler until processing.

The contents of each sample bag were dissected and washed in a tagged collecting strainer, and the strainer was placed for three minutes in a dish pan containing a saturated salt solution with a specific density of 1.17 at 15.5°C. The saturated salt solution was used to increase the specific gravity of the solution so as to facilitate recovery of insect predators. The insects floating in the salt solution were removed with a water suction aspirator attached to a filtering flask.

The solution containing the insects was poured from the filtering flask into a Buchner funnel. As soon as the salt solution was removed, the sample was washed with 70% ETOH into a 59.1 ml screw cap bottle. At the conclusion of each sampling period, insects from each jar were examined, identified, and their numbers recorded.

Analysis of variance was computed on each insect predator group. The treatment, dates, and treatment x date predator means were then compared for significant differences by using Duncan's multiple range test.

RESULTS AND DISCUSSION

Orius insidiosus adults were not significantly reduced (at 5% level) by any treatment in 1970 or 1971 on early planted corn (Table 1). Plots treated with carbofuran granules, however, showed a significant increase in number of adults. This situation, occurring in both years, is unexplainable.

In 1970 and 1971, all granular insecticides lowered the *Orius insidiosus* nymph population over the entire sampling period in early planted corn (Table 1). One spray

Table 1. Effect of insecticides applied as granular and spray formulations on *Orius insidiosus* on field corn, Ankeny, Iowa.

Material ^a and formulation	Mean no./plants ^b									
	Early Planting		Late Planting		Early Planting		Late Planting			
	1970, 32 samples		1970, 112 samples		1971, 64 samples		1971, 120 samples			
	kg AI/ha	Adults	Nymphs	Adults	Nymphs	Adults	Nymphs	Adults	Nymphs	
Carbofuran	G	0.56	4.9b	1.4ab	6.9d	1.2bc	6.9c	1.5ab	19.5e	3.0b
	Sp	0.56	3.6a	2.2c	5.3bcd	0.6ab	4.3a	2.4cde	14.3cd	1.5a
Diazinon	G	1.12	3.9a	1.3a	3.8ab	0.8ab	5.5b	1.3a	15.1d	1.3a
	Sp	1.12	3.1a	2.2c	4.9abcd	0.5ab	4.1a	2.6e	10.8b	2.2ab
EPN	G	0.56	3.7a	1.3a	6.1cd	1.1bc	5.7b	1.6ab	11.1bc	2.8b
	Sp	0.56	3.7a	2.7c	5.3bcd	0.3a	4.0a	2.0bcd	11.9bcd	2.0a
DDT	G	1.12	3.3a	1.7ab	5.7bcd	1.5cd	3.7a	1.2a	9.2ab	2.9b
	Sp	1.12	3.3a	1.8bc	3.0a	0.3a	4.2a	1.9bc	9.3ab	1.7a
Untreated			3.7a	2.4c	4.7abcd	2.1d	3.9a	2.5de	7.3a	4.8c

^aG = granular formulation; Sp = spray formulation.^bMeans followed by the same letter are not significantly different at the 5% level of probability, Duncan's multiple range test.

Table 2. Effect of insecticides applied as granular and spray formulations on coccinellids on field corn, Ankeny, Iowa.

Material ^a and formulation			Mean no./plants ^b							
			Early Planting		Late Planting		Early Planting		Late Planting	
			1970, 32 samples		1970, 112 samples		1971, 64 samples		1971, 120 samples	
		kg AI/ha	Adults	Larvac	Adults	Larvac	Adults	Larvac	Adults	Larvac
Carbofuran	G	0.56	0.41a	0.38cd	0.53a	0.06a	0.38a	0.08a	0.48b	0.58a
	Sp	0.56	0.23a	0.15a	0.31a	0.12a	0.23a	0.18a	0.14a	0.17a
Diazinon	G	1.12	0.28a	0.24ab	0.77a	0.09a	0.27a	0.30a	0.34ab	0.33a
	Sp	1.12	0.25a	0.24ab	0.34a	0.00a	0.21a	0.07a	0.39ab	0.36a
EPN	G	0.56	0.27a	0.37cd	0.34a	0.03a	0.30a	0.08a	0.26ab	0.31a
	Sp	0.56	0.21a	0.28bc	1.09b	0.06a	0.24a	0.17a	0.22a	0.19a
DDT	G	1.12	0.34a	0.80e	0.53a	0.06a	0.29a	0.07a	0.15a	0.36a
	Sp	1.12	0.23a	0.45d	0.28a	0.08a	0.22a	0.13a	0.27ab	0.52a
Untreated			0.45a	0.46d	0.28a	0.18a	0.38a	0.18a	0.54b	0.53a

^aG = granular formulation; Sp = spray formulation.^bMeans followed by the same letter are not significantly different at the 5% level of probability, Duncan's multiple range test.

formulation, DDT, in 1971 also significantly lowered the nymph population.

Greater reduction of the population by the granular treatments was thought to be due to the larger amounts of toxicant reaching the whorl area. Spray formulations, on the other hand, tended to adhere to the surface with little penetration to the whorl. Since the nymphs were primarily in the whorl at the time of application, their chance of contact with the granules increased.

Combined results from all sampling dates of *Orius insidiosus* adults on late planted corn showed that the treated and untreated plots were not significantly different in 1970 (Table 1). In 1971, plots treated with carbofuran, diazinon, and EPN in both formulations had a significantly higher population of adults than did the untreated plots; this, also, is not explained.

In both 1970 and 1971, all treatments except DDT granules significantly reduced the *Orius insidiosus* nymph population on late planted corn. Numerically, sprays were more toxic to the nymphs than the granular formulations. This situation was a complete reversal from what was reported for nymphs on early planted corn (Table 1) in which the granular formulations were significantly more toxic. Nymphs on late planted corn were located in exposed areas when the chemicals were applied. Thus, the chance of contact with the toxicant (spray formulation) was increased.

The three major coccinellids found in this study were *Chrysopa maculata*, *Hippodamia convergens*, and *H. tetricimpunctata tibialis* (Say). These coccinellids were combined into a single group for evaluation because of low numbers.

The number of coccinellid adults on early planted corn in treated plots showed no significant reduction of the population for the overall sampling period in 1970 and 1971 (Table 2). However, the coccinellids present in these plots did show numerical variations. In 1970, all insecticide plots showed a numerical reduction of coccinellid adults when compared with the untreated plots. The spray formulation for both years appeared to be more deleterious to these coccinellids than did the granular formulations. Of all formulations, the plots treated with carbofuran granules showed the least reduction of adults for both years.

A comparison of the number of coccinellid larvae on early planted corn in the treated plot for the overall sampling period in 1970 showed significant larval reductions in the treated plot (Table 2). In this comparison, carbofuran, diazinon, and EPN as sprays along with a granular formulation of diazinon reduced the larval population significantly. Data collected in 1971 showed no significant differences due to treatments.

The number of adults in treated and untreated plots on late planted corn in 1970 did not show any significant reductions in populations due to insecticides (Table 2). This lack of toxic effect may have been the result of removal of the insecticide by heavy rainfall (ca 5 cm shortly after insecticide application on August 2). In 1971, however, there were significant differences. Numbers of adults were significantly reduced by carbofuran and EPN sprays and DDT in granular formulation. Numerically, all plots showed reductions of coccinellid adults in 1971.

The number of larvae in treated and untreated plots for the combined individual sampling dates for 1970 and 1971 showed no significant differences on late planted corn (Table 2). This situation resulted from low overall infestations and toxicant removal by rainfall.

The other corn borer predators found in this study were the following: *Chrysopa* spp., including *C. carnea* Stephens and *C. oculata* Say; and *Nabis* spp., including *N. roseipennis* Reuter, *N. alternatus*, and *N. ferus* (L.). Although these were found in low numbers during this study, evaluation was necessary to furnish a total overview of possible insecticide effects on the insect predator populations.

In the evaluations of the effects of the insecticides on *Chrysopa* spp., only 0 to 0.14 mean numbers of adults and larvae/plant/planting time were recorded. These low values made it impossible to show even numerical trends as to insecticide effects. The *Nabis* spp.

results were basically the same as those reported for the *Cbrysopa* spp. No significant mean differences or trends were evident for either year or time of planting.

LITERATURE CITED

- Hill, R.E. 1945. Effects of DDT and other insecticides on several species of potato insects. Neb. Agric. Exp. Sta. Res. Bull. 138: 3-14.
- Johansen, D. and J. Eves. 1967. Systemic insecticides as lygus bug controls compatible with bee pollination on alfalfa. J. Econ. Ent. 60: 1690-1696.
- McFarland, V.L. 1963. A quantitative evaluation of insect predators found on corn. Unpublished M.S. thesis, Iowa State University of Science and Technology. 104 pp.
- Ripper, W.E. 1956. Effect of pesticides on balance of arthropod populations. Ann. Rev. of Ent. 1: 403-438.

GENETIC CONTROL OF IRON DEFICIENCY CHLOROSIS IN SOYBEANS¹

S. Rodriguez de Cianzio and W.R. Fehr²

ABSTRACT. Soybean (*Glycine max*) cultivars differ in their response to iron deficiency chlorosis on calcareous soils. Our objective was to determine the genetic basis for the varying degrees of resistance expressed under field conditions. A resistant line, IVR EX-5003, was crossed to a susceptible cultivar, 'Anoka,' and four backcrosses were made to IVR EX-5003 and one to Anoka. The parents and 60 lines derived from the F₂ and each of the five backcross generations were evaluated on calcareous soil by a visual rating and by determination of chlorophyll concentration.

The observed segregation can be explained by a single major gene and modifying genes. The F₂-derived lines in F₄ satisfactorily fit a ratio of 1 homozygous resistant : 2 segregating : 1 homozygous susceptible. The frequency of segregating lines decreased with each generation of backcrossing in the proportion expected for a single major gene. The distribution of BC₁F₁ lines with chlorosis ratings intermediate to that of the parents was skewed toward the recurrent parent used in the backcross which indicated that modifying genes were present.

INTRODUCTION

Soybean (*Glycine max*) cultivars differ in the amount of iron deficiency chlorosis expressed on calcareous soils. Continuous variation ranges from cultivars that have leaf necrosis and plant mortality to those that remain completely green. Susceptibility to iron chlorosis is a factor considered by farmers in selecting cultivars for calcareous soils (Clark et al., 1971).

Inheritance of iron utilization in soybeans tested in a nutrient solution with a low concentration of iron was reported by Weiss (1943) to be controlled by a single gene with the allele for efficiency, *Fe*, dominant to the allele for inefficiency, *fe*. He said that the simplicity of the genetic control was remarkable considering the complex nature of mineral absorption and utilization in plants. He also found variation in iron efficiency among inefficient varieties, but believed that the effect of modifying genes was negligible in comparison with that of the major gene. Brown et al. (1967) stated that *Fe* is dominant to *fe* under field conditions, but may be modified by other factors. They did not provide any data, however, to support their statement.

It is not possible to account for the known range of chlorosis susceptibility among soybean cultivars with a single major gene, unless modifying genes substantially influence its expression. The objective of our research was to evaluate the genetic control of iron chlorosis under field conditions and its implication for selection procedures.

¹Joint contribution from the Iowa Agricultural and Home Economic Experiment Station, Ames, Iowa, Journal Paper No. J-9257, Project No. 2118; and the University of Puerto Rico, Mayaguez, Puerto Rico. The research was supported in part by a grant from the Iowa Soybean Promotion Board.

²Assistant Professor and Professor of Agronomy, Iowa State University, Ames, Iowa 50011.

MATERIALS AND METHODS

A resistant and susceptible cultivar were chosen for the study on the basis of performance in Iowa tests on calcareous Harps soil (Clark et al., 1971). The first was IVR EX-5003, abbreviated herein as I5003, an experimental line of Group I maturity obtained from Improved Variety Research, Inc., Adel, Iowa, which had the best chlorosis resistance of any available line. The susceptible cultivar chosen, Anoka (Lambert, 1971), is of Group I maturity, has severe chlorosis symptoms, and is unrelated to I5003.

Lines were derived from the F_2 generation of Anoka \times I5003, four backcross generations with I5003 as the recurrent parent, and one backcross generation with Anoka as the recurrent parent. The cross of Anoka \times I5003 was made at Isabela, Puerto Rico, in February 1975. F_1 plants were grown at Ames in the summer, and 70 BC_1 seeds were obtained for Anoka \times I5003², designated I5003 BC_1 , and for Anoka² \times I5003, designated Anoka BC_1 . F_2 seeds harvested from the F_1 plants were placed in cold storage. No further backcrosses were obtained with Anoka.

For the second backcross to I5003, designated I5003 BC_2 , at least four BC_2F_1 seeds were obtained on each of 60 BC_1F_1 plants at Isabela during December 1975. Each BC_1F_1 plant and the BC_1F_2 and BC_2F_1 seed from them were identified with a family number. The family structure was maintained during subsequent backcrosses so that the lineage of each backcross line could be identified in the final evaluation.

The third backcross, designated I5003 BC_3 , was obtained at Isabela during February 1976. At least four BC_3F_1 seeds were obtained on one BC_2F_1 plant in each family, and the BC_2F_2 seeds from the plant were harvested. The fourth backcross, designated I5003 BC_4 , was obtained at Ames during the summer. At least four BC_4F_1 seeds were obtained on one BC_3F_1 plant in each family, and the BC_3F_2 seeds from the plant were harvested. The BC_4F_1 seeds and 120 F_2 seeds were planted at Isabela in October 1976. One random BC_4F_1 plant was harvested from each family. Sixty F_2 plants also were harvested individually.

Seeds from plants of the F_2 , all backcross generations, and the parents were increased at Isabela during January to May of 1977. Fifty seeds from each plant were grown in a single row and each row was harvested in bulk.

Most genetic studies include an evaluation of individual plants in the F_2 and backcross generations, followed by a progeny test. In our study, evaluation of individual plants in the field was hampered by the effect of soil heterogeneity on chlorosis expression. A replicated progeny test was used instead of individual plant analysis, and mean performance of plants in each plot was determined.

A test of 400 entries was planted on 13 May 1977 at Ames and Knierim, Iowa, on Harps soil where chlorosis symptoms had been expressed consistently in previous years. Soil pH was 7.4 at Ames, and 7.9 at Knierim, as measured in a 1:2, soil: water paste. The entries consisted of 60 F_2 -derived lines in the F_4 , 60 Anoka BC_1F_1 -derived lines in the F_3 , 60 I5003 BC_1F_1 -derived lines in the F_3 , 60 I5003 BC_2F_1 -derived lines in the F_3 , 60 I5003 BC_3F_1 -derived lines in the F_3 , 60 I5003 BC_4F_1 -derived lines in the F_3 , eight duplicate samples of I5003, Anoka, and three check cultivars, 'Amsoy 71,' 'Corsoy,' and 'Hawkeye' that were chosen to represent cultivars with intermediate chlorosis resistance to that of I5003 and Anoka.

The 400 entries were subdivided into four sets of 100 to reduce the effects of soil heterogeneity on the comparison of family means across backcross generations. Each set included four backcross generations from 15 families with I5003 as recurrent parent, 15 Anoka BC_1 lines, 15 F_2 lines, two samples of Anoka I5003, and the three check cultivars. The four sets were randomized as blocks in three replications at each location. The 100 entries within each set were randomized as a 10 \times 10 lattice design. Single-row plots 1.5 m long with 68 cm between rows were planted with 40 seeds of an entry.

Chlorosis symptoms were rated by visual scores (Vs) and total chlorophyll concentration (Cab). Visual scores were based on yellowing of the first fully developed trifoliolate

leaf at the second-node stage (V2)(Fehr et al., 1971). The ratings were: 1 no yellowing, 2 slight yellowing, 3 moderate yellowing, 4 intense yellowing, and 5 severe yellowing with some necrosis. Plots were rated as an estimate of the average of plants to the nearest 0.5 score.

Leaves were harvested for chlorophyll extraction the day after scores were assigned. The first trifoliolate leaf was harvested from the first 10 plants in each plot, placed in a plastic bag, stored in an ice chest, and transported to the laboratory. A leaf disc was obtained with a cork borer of 9 mm diameter from the middle leaflet of each of the 10 leaves. The discs were placed in a test tube and 10 ml of 80% acetone were added. The solution was heated in a water bath at 65 C for 10 min; then 80% acetone was added to bring the total volume to 25 ml and every tube containing the leaf discs in solution was covered and left 12 hours in the dark before readings were taken.

A 10 ml sample of the acetone solution was poured into a tube used with the Spectronic 20 Bausch & Lomb spectrophotometer. Absorbancy readings for chlorophyll a (Ca) and chlorophyll b (Cb) were measured on two spectrophotometers; one set at 663 mu for Ca and the other at 645 mu for Cb. Ca, Cb, and total chlorophyll (Cab) concentration in mg dm⁻² were computed with equations derived by Arnou as cited by Bruinsma (1963).

$$Ca = 12.7 A_{663} - 2.7 A_{645}$$

$$Cb = 22.9 A_{645} - 4.7 A_{663}$$

$$Cab = 20.2 A_{645} + 8.0 A_{663}$$

The data from each set were analyzed separately as a lattice design, and adjusted entry means were obtained for Vs, Ca, Cb, and Cab at each location and combined as described by Cochran and Cox (1957). Ca, Cb, and Cab were found to be highly correlated, and only Cab data will be discussed herein. (Cianzio et al., 1979).

Parents and checks common to the four sets were used to estimate differences among sets. Sets were considered as whole plots and parents and checks as subplots. No significant differences were observed among sets for any character; therefore, sets were ignored and the 400 entries analyzed as a randomized complete block design. Lines within generations and locations were considered random effects, and parents and checks fixed effects.

RESULTS

The frequency distribution for Vs of the F₂ lines was continuous, within the range of the parents, and bimodal (Fig. 1). The two most frequent classes for the F₂ lines were the same as the most frequent classes for the parents. The distribution of F₂ lines on the basis of Cab was continuous, with a mode intermediate to the parents (Fig. 2). For both traits, the frequency of lines similar to the recurrent parent increased with each generation of backcrossing.

The distribution of lines in each generation was evaluated under the assumption that chlorosis resistance was controlled by a single major gene, as proposed by Weiss (1943). Lines with a Vs or Cab within the range of I5003 were considered an homozygous resistant, those within the range of Anoka as homozygous susceptible, and those with intermediate scores as segregating (nonparental lines). The expected ratio in the F₂ was 1 resistant : 2 segregating : 1 susceptible. Expected frequency of the homozygous parental types in the back-cross generations was calculated with the formula $(1 - \frac{1}{2^n})$, where n was the number of

crosses to the recurrent parent. The expected frequency of segregating lines was $(\frac{1}{2^n})$.

There were no significant differences between observed and expected frequencies for data based on Vs (Table 1). Similar results were observed for Cab, except for I5003BC₁ (Table 2). The significant deviation in this generation was due to a higher number of lines than expected within the range of I5003. For Cab, there was a general trend for all generations except I5003BC₄ to have more lines than expected within the range of I5003. The deviation may have been caused by the effect of susceptible plants that escaped chlorosis and remained green due to soil heterogeneity. Cab was based on 10 plants and one or two green susceptible plants could have shifted the plot mean toward I5003. Similar plants would have less effect on Vs, which is based on the average appearance of up to 40 plants in each row.

The single-gene model was evaluated further by examining the change in Vs and Cab for each I5003 family from BC₁ to BC₄. With a single gene model, 50% of the BC₁ families would be homozygous for the gene of I5003 and have similar Vs and Cab to the recurrent parent. The remaining 50% of the BC₁ families would be derived from heterozygous BC₁F₁ plants, and their Vs and Cab would be inferior to I5003. With each subsequent backcross, the frequency of homozygous families would increase by 50% of heterozygous plants in the previous generation.

The observed changes in I5003 families during backcrossing supported the single gene model. There were 33 BC₁ families (55%) similar to I5003 for both Vs and Cab. In the BC₂, 12 (44%) of the 27 remaining families improved to the level of I5003. Of the remaining 15 BC₂ families, 5 (33%) improved in the BC₃ and 4 (40%) of the remaining 10 BC₃ families improved in the BC₄.

The single-gene model also was evaluated by comparing the frequency distribution of I5003BC₁ lines with Anoka BC₁ lines. If only one major gene determines chlorosis resistance, the frequency distribution for segregating lines should be similar, regardless of the cultivar used as the recurrent parent. We observed, however, that the distributions of segregating lines were skewed toward the cultivar used as the recurrent parent (Figs. 1 and 2). There were 33% of the AnokaBC₁ lines with a Vs of 4.0 to 4.5 compared with only 8% for I5003BC₁. Conversely, 30% of the I5003BC₁ lines had Vs of 3.0 to 4.0 compared with only 9% for AnokaBC₁. The least frequent class of segregating lines for I5003BC₁ on the basis of Cab was the most frequent class for AnokaBC₁. The difference in the distribution of segregating lines for AnokaBC₁ and I5003BC₁ indicated that expression of the single major gene is influenced by modifying genes in the recurrent parents.

The influence of environment and modifying genes on chlorosis expression suggested that resistance to chlorosis may be considered as a quantitative character in breeding programs. Broad-sense heritability estimates were computed for Vs and Cab based on variance component estimates for F₂ lines as proposed by Fisher and described by Crump (1946). Heritabilities on a plot basis were 0.73 for Vs and 0.42 for Cab, and on an entry-mean basis were 0.91 for Vs and 0.74 for Cab. The heritability values indicated that selection should be effective with limited testing on appropriate soils.

DISCUSSION

I5003 and Anoka represented the extremes in chlorosis expression observed among commercial cultivars available when the study was initiated. Our data indicated that the two parents differed by a major gene and modifying genes. Such a genetic system could explain the range of resistance to iron chlorosis observed among soybean cultivars.

The major gene in I5003 and other resistant lines probably is the *Fe* gene observed by Weiss (1943) in 'Dunfield,' 'Mandell,' 'Illini' and 'Mukden' and by W.D. Hanson (Brown et al., 1967) in 'Hawkeye.' In 1975, we selected 10 commercial cultivars, including I5003,

Table 1. Chi-square test for goodness of fit to a ratio of 1 homozygous resistant : 2 segregating : 1 homozygous susceptible for lines evaluated in a progeny test for visual chlorosis score.

Generation	CHLOROSIS SCORES ^a						χ ^{2b}
	1.8 to 2.6		2.7 to 4.5		4.6 to 5.0		
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	
F ₂	17	15	30	30	13	15	0.53
AnokaBC ₁	1	0	24	30	35	30	2.03
I5003BC ₁	31	30	28	30	1	0	0.17
I5003BC ₂	43	45	17	15	—	—	0.35
I5003BC ₃	48	52.5	12	7.5	—	—	3.08
I5003BC ₄	53	56.25	7	3.75	—	—	3.00

^aThe parental classes correspond to the range for I5003 of 1.8 to 2.6 and for Anoka of 4.6 to 5.0. The nonparental class was intermediate between the parents, 2.7 to 4.5.

^bNone of the χ^2 values exceeded the 5% probability level.

Table 2. Chi-square test for goodness of fit to a ratio of 1 homozygous resistant : 2 segregating : 1 homozygous susceptible for lines evaluated in a progeny test for total chlorophyll concentration.

Generation	CHLOROPHYLL CONCENTRATION ^a						χ ²
	1.6 to 2.2		0.9 to 1.5		0.5 to 0.8		
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	
F ₂	21	15	30	30	9	15	4.80
AnokaBC ₁	5	0	28	30	27	30	0.43
I5003BC ₁	43	30	17	30	—	—	11.27 ^b
I5003BC ₂	51	45	9	15	—	—	3.20
I5003BC ₃	54	52.5	6	7.5	—	—	0.34
I5003BC ₄	55	56.25	5	3.25	—	—	0.97

^aThe parental classes correspond to the range for I5003 of 1.6 to 2.2 and for Anoka of 0.5 to 0.8. The nonparental class was intermediate between the parents, 0.8 to 1.5.

^bValue significant at the 1% probability level.

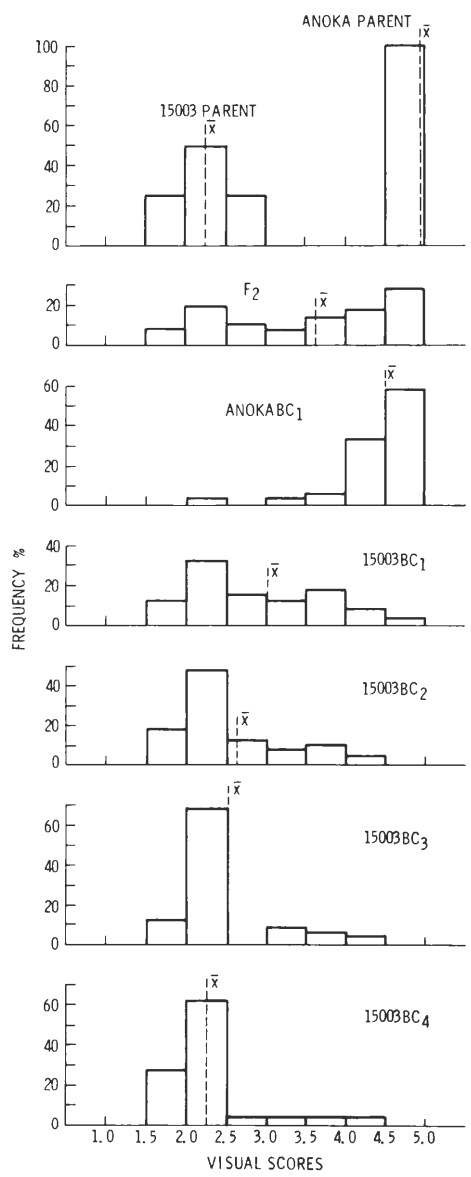


Figure 1. Frequency distribution of visual chlorosis scores averaged across locations and means for 15003, Anoka, and lines derived from the F₂ and five backcross generations.

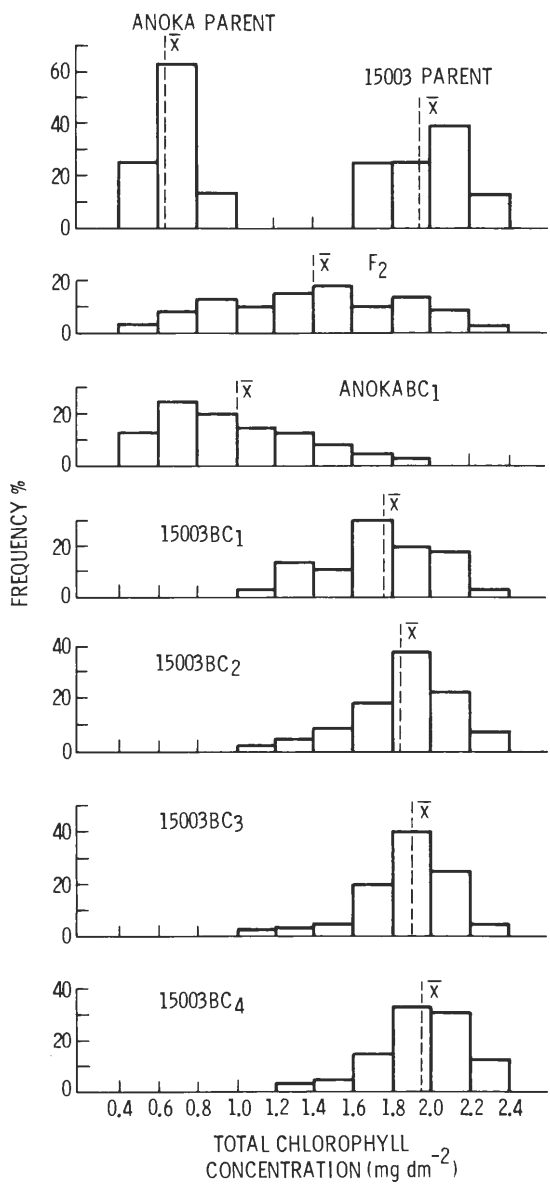


Figure 2. Frequency distribution of total chlorophyll concentrations averaged across locations and means for 15003, Anoka, and lines derived from the F₂ and five backcross generations.

and 10 plant introductions with an average chlorosis rating superior to Hawkeye. Each line was crossed at random to one other, and their progeny advanced to the F_4 generation by single-seed descent. None of the F_4 -derived lines evaluated from the crosses had 2Vs worse than Hawkeye, indicating that the *Fe* allele probably was present in the lines.

It is not known if the allele of the major gene in Anoka is the same *fe* allele present in the six plant introductions studied by Weiss (1943). Crosses of Anoka with the inefficient lines of Weiss (1943) have not been made.

The presence of modifying genes for chlorosis resistance is typical of the interrelationship of major and minor genes for many soybean characters, such as time of maturity (Bernard, 1971). Modifying genes for chlorosis resistance would explain the relative iron efficiency of lines studied by Brown et al. (1967). They used two isolines developed from the cross of PI 54619-5-1 x Hawkeye and the original parents. The isolines were developed by selecting for a *Fefe* plant during several generations of selfing, then identifying an *FeFe* and *fe* plant from its segregating progeny. They found that Hawkeye was more efficient than the *FeFe* isoline, and the PI was equal or superior to the *fe* line.

The similarity in results obtained by use of Vs and Cab occurred when plants expressed a broad range of chlorosis symptoms on calcareous soils. Our results do not indicate that response to iron deficiency chlorosis is controlled by the same genetic system as that controlling chlorophyll concentration of healthy soybeans. The inheritance of chlorophyll concentration of healthy soybeans would require the evaluation of plants under chlorosis-free conditions.

Backcrossing should be an effective means of transferring the major gene from a resistant to a susceptible cultivar. A replicated progeny test on appropriate calcareous soils before each backcross should improve the probability of recovering favorable modifying genes from the resistant parent. The use of visual ratings should be adequate for selection. Visual ratings are as effective as, and much less time consuming than, determination of total chlorophyll concentrations for direct comparison of genotypes. (Cianzio et al., 1979).

Selection for chlorosis resistance superior to that of existing genotypes may be possible because of variability among the modifying genes. A recurrent selection program has been initiated to determine the extent to which chlorosis resistance can be improved.

LITERATURE CITED

- Bernard, R.L. 1971. Two major genes for time of flowering and maturity in soybeans. *Crop Science* 11: 242-244.
- Brown, J.C., C.R. Weber, and B.E. Caldwell. 1967. Efficient and inefficient use of iron by two soybean genotypes and their isolines. *Agron. J.* 59: 459-462.
- Bruinsma, J. 1963. The quantitative analysis of chlorophylls a and b in plant extracts. *Photochem. and Photobiol.* 2: 241-249.
- Cianzio, S. Rodriguez de, W.R. Fehr, and I.C. Anderson. 1979. Genotypic evaluation for iron deficiency chlorosis by visual scores and chlorophyll concentration. *Crop Science* 19: 644-646.
- Clark, R.C., W.R. Fehr, D.L. Gedge, and D.R. Ivers. 1971. Iowa soybean yield test report. Iowa State Univ., Coop. Ext. Serv. AG18-1.
- Cochran, W.G., and G.M. Cox. 1957. *Experimental designs*. John Wiley. New York.
- Crump, S.L. 1946. The estimation of variance components in analysis of variance. *Biom. Bull.* 2: 7-11.
- Fehr, W.R., C.E. Caviness, D.T. Burmood, and J.S. Pennington. 1971. Stage of development descriptions for soybeans, *Glycine max* (L.) Merrill. *Crop Science* 11: 929-931.
- Lambert, J.W. 1971. Registration of 'Anoka' soybeans. *Crop Science* 11: 135.
- Weiss, M.G. 1943. Inheritance and physiology of efficiency in iron utilization in soybeans. *Genetics* 28: 253-268.

MAINTENANCE OF SOYBEAN SEED QUALITY IN STORAGE AS INFLUENCED BY MOISTURE, TEMPERATURE AND GENOTYPE¹

J.S. Burris²

ABSTRACT. Soybeans were stored three years at seed moisture levels of 8, 10, 12, and 14% and storage temperatures of -1, 10, 15, 20, and 27 C, and the effects of seed quality were determined. Seeds were also stored for one year to evaluate the genotypic response observed in the main experiment. Though there were significant genotypic effects for germination and vigor, those were of lesser magnitude than the other variables and were not considered in the calculation of predictive constants. The practice of harvesting soybeans at high moisture levels (14%) restricts storage life to one season. Extended storage of high-value, low-volume seed can be accomplished by reducing the moisture content to 8–10% and/or reducing the storage temperature. The genotypic effect on storability which was correlated with vigor (seedling growth rate) suggests that selection for vigor may also improve storability.

INTRODUCTION

Safe, economical soybean (*Glycine max* L.) seed storage has been a problem for both seedsmen and growers. In general, the practice of storing soybean seed beyond six-nine months has not been recommended. As the value of soybean seed has increased, however, the economic incentives to carry over seed have increased. In addition, foundation seed producers must maintain small quantities of seed of a large number of genotypes for several years. Previous studies of soybean storage usually include only one environmental variable, and genotype is seldom considered a treatment. Byrd and Delouche (1971) reported on the storability of soybean seed that had been artificially aged. The storage portion of their study, maintained nine months, allowed them to evaluate various predictive tests but not storage conditions. While the report by Toole and Toole (1946) includes both temperature and moisture, genotypic variability was scarcely sampled. Harrington (1963) developed the rule of thumb which states that, for each 1% reduction in seed moisture content the storage life of seed is doubled and, for each 5 C decrease in storage temperature, the storage life of the seed is doubled. This generalization is based on data from studies on several kinds of seeds. Roberts (1972) reviewed several models and storage prediction equations. These equations represent estimates of the influence of temperature and moisture on the maintenance of seed quality during storage. Roberts (1960, 1972) suggested that the equation:

$$\log p_{50} = K_v - C_1 m - C_2 t, \text{ where}$$

p_{50} = the ½ viability period, m = moisture constant, t = temperature °C, and K_v , C_1 and C_2 are constants, provided a reasonable fit to the experimental data available at that time. Hukill (1963) described the relationship between viability and storage environment by developing an "age index":

¹Journal Paper No. J-9360 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa. Project 2191.

²Professor, Department of Plant Pathology, Seed and Weed Sciences, Iowa State University, Ames, Iowa 50011.

$$\text{age index} = \text{months in storage} \times 10^{0.143mc} \times 10^{0.0645T}$$

where mc = moisture content (%) and T = temperature (°C). His graphs relate quite well to the germination figures used, namely the 1946 data of Toole and Toole.

The present study attempts more completely to define the relationship between storability and genotype, moisture, temperature, and time in storage.

METHODS AND MATERIALS

Seed was obtained from 1972 production of the Committee for Agricultural Development, Ames, Iowa. Varieties used were 'Amsoy,' 'Beeson,' 'Calland,' 'Corsoy,' 'Hawkeye' and 'Wayne.' The lots were divided into four sublots which were equilibrated to either 8, 10, 12, or 14% moisture. The desired moisture levels were obtained by exposure of the seed to either 10% RH at 25 C or 90% RH at 5 C. After the seed had attained the desired moisture percentage, a quantity sufficient for all the tests for a given sampling period was sealed in a three mil polyethylene bag. The 12 packages required for the entire study were sealed in a polypropylene container to ensure maintenance of seed moisture content. On May 1, 1973, containers were transferred to temperature chambers maintained at -1.1, 10, 15, 20, and 27 C and remained there for the next 36 months. Samples were removed at three-month intervals. The seed moisture content (oven dry weight basis), germination and vigor were determined at each sampling period. Germination and vigor were determined from a modified rolled towel test as described in the Association of Official Seed Analysts (AOSA) Newsletter (1976). The cotyledons from the normal seven-day-old seedlings were discarded, the roots and shoots were separated and dried at 80 C for 24 hours. The sample dry weight was divided by the number of normal seedlings and reported as an estimate of vigor.

A one-year study was established using four seed lots each of Amsoy and Calland soybeans. Sublots were equilibrated to 8% and 14% moisture, then sealed and stored for one year at 20 C with samples removed at three-month intervals. The same parameters were measured on each sample as in the main experiment.

RESULTS AND DISCUSSION

The difference between initial and final moisture content was less than 0.5 percentage points and on analysis of variance showed no significant change in moisture content during the three-year study; thus the results of the moisture content determination are not reported. The double-sealing procedure proved to be a simple and effective way of maintaining a constant seed moisture content over an extended period.

The germination and shoot weight of each variety averaged over moisture and temperature during the 36-month period are reported in Figures 1 and 2. The six varieties are grouped into two classes. Wayne and Calland deteriorated at slower rates than did the other varieties. The rate difference is especially pronounced between dates one and two; thereafter, the rates were quite similar. The vigor differences due to genotype were less pronounced (Figure 2), and a significant genotype effect was difficult to differentiate from a seed lot effect. The results of the analysis of variance of the one-year study (Table 1), and the main experiment results given in Figure 3, however, show a significant varietal response. The magnitude of the genotype response is of doubtful biological significance, as indicated by the similarity of the curves (Figure 3). Both varieties showed no change in germination through the first three months of storage. This was followed by a marked decrease during the next six months, and then a leveling off between nine and twelve months after initial storage. The vigor (shoot weight) differences between varieties were greater than the germination differences, but vigor reduction followed a similar pattern among varieties.

Table 1. Analysis of variance in germination of a one-year study as affected by genotype, seed lot, and moisture content averaged across dates.

Source	d.f.	Mean Squares ¹
Genotype	1	575.8*
Lot	3	1,975.5**
Genotype x Lot	3	280.0
Moisture	1	189,458.6***
Genotype x Moisture	1	605.9*
Lot x Moisture	3	996.6*

¹F value significant at the 0.05 = *, 0.01 = **, and 0.001 = ***.

The decreases in germination with time in storage as affected by moisture content (Figure 4) were a “family” of first order curves. The decrease in germination as influenced by moisture content over time was nearly linear. Thus if 70% germination is assumed to be the minimum acceptable value, then one year appears to be the maximum safe storage period possible at either 12% or 14% seed moisture content. The seed held at 8% seed moisture exhibited a satisfactory germination after 36 months. Storability at 10% seed moisture was intermediate between 8% and 12%.

The effects on germination of storage temperature averaged across moisture and variety (Figure 5) show that storage at 20 C and 27 C reduced germination much more rapidly than did storage at 10 or 15 C. The decrease was exponential at the higher temperatures and nearly linear at the lower temperatures. Storage at -1 or 10 C caused only a slight change in germination over three years. Germination changes during storage at the lower two temperatures did not follow a statistically normal distribution as indicated by the lack of linearity when plotted on probability paper. This presumably suggests that the aging processes under low temperature conditions are different from those under high temperature.

The changes in vigor (shoot weight) as affected by moisture and temperature (Figure 7) and storage period across varieties (Figure 6) are not as pronounced as those exhibited by the germination values. This may be because, in calculating vigor, only those seedlings considered normal were harvested for the dry-weight determination; i.e., those seedlings which maintain the capacity to germinate also maintain a reasonable level of vigor.

A significant genotypic effect on storability has seldom been reported in the literature. The existence of genotypic effects complicates the development of predictive constants for storability. In this study the predictive constant calculations were made across varieties. Using the method outlined by Roberts (1972), we found the constants to be: $K_v = 4.414$, $C_1 = 125$, and $C_2 = 0.062$. These are based on a limited amount of data because of the non-normal distribution of the low-temperature and low-moisture data (Figure 8). These constants indicate that soybeans have a shorter life span than rice, barley, and broadbeans, but longer than wheat at the same storage conditions. This

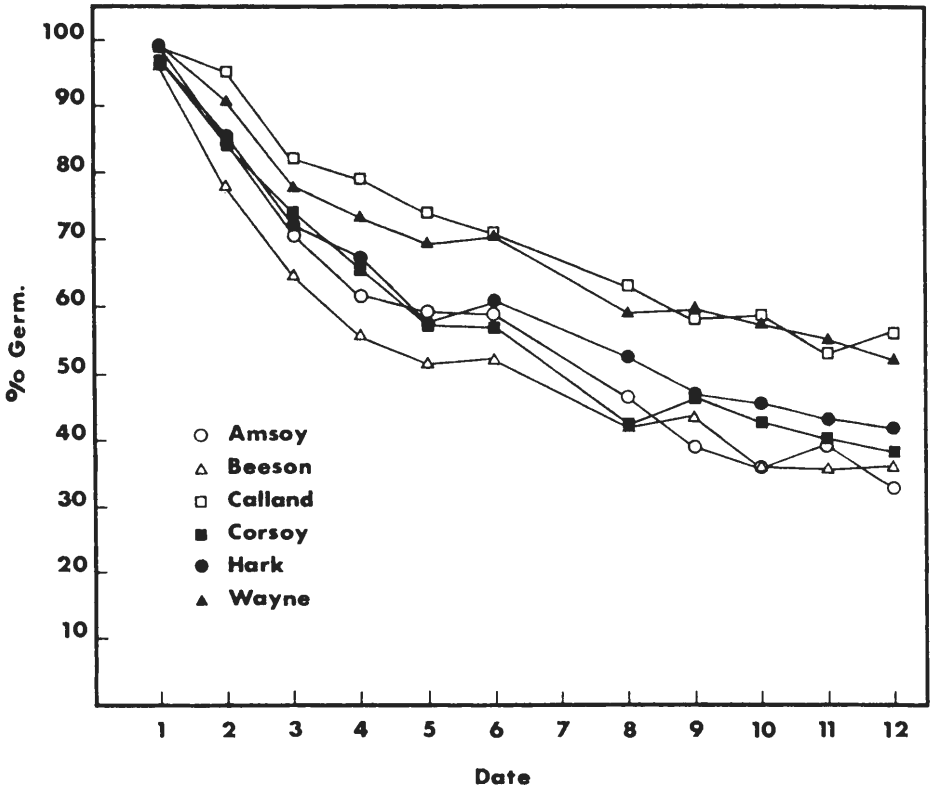


Figure 1. Effects of variety on germination percentage averaged across temperatures and moistures sampled at three-month intervals.

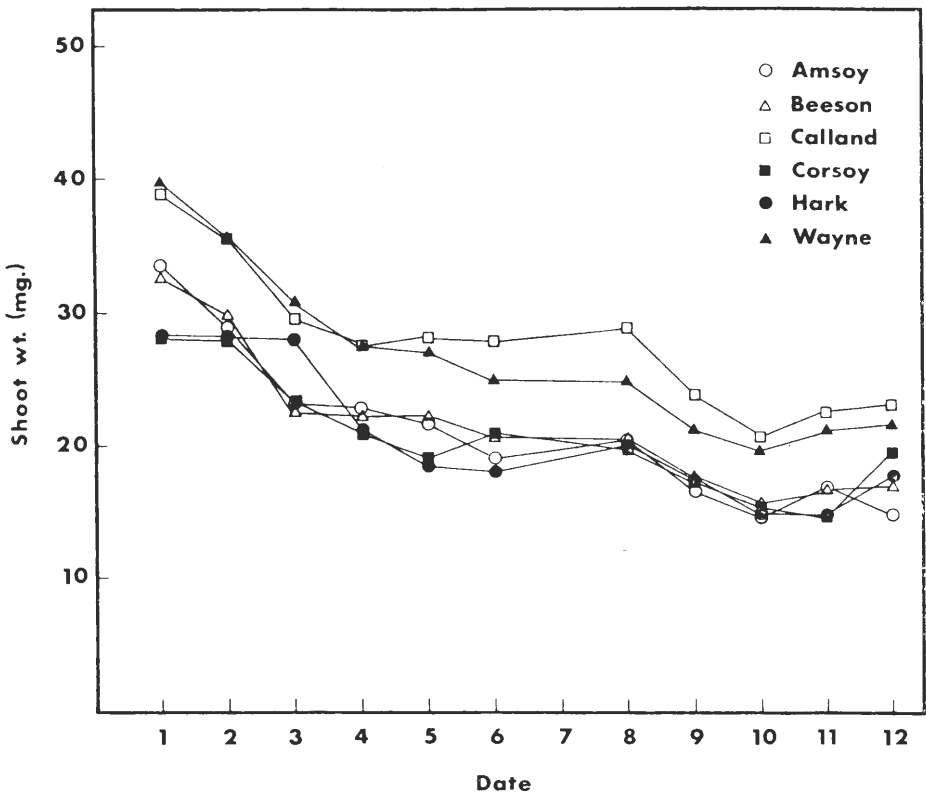


Figure 2. Effects of variety on shoot weight averaged across temperatures and moistures sampled at three-month intervals.

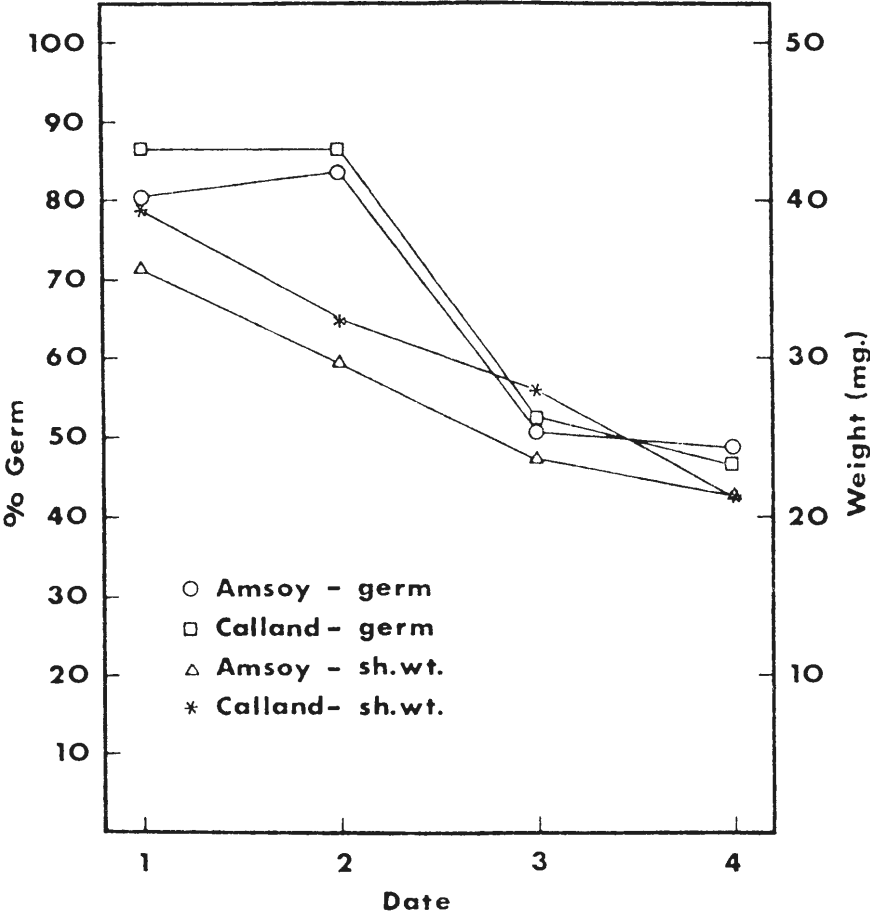


Figure 3. Effects of variety on germination percentage and shoot weight averaged across moistures and seed lots sampled at four-month intervals.

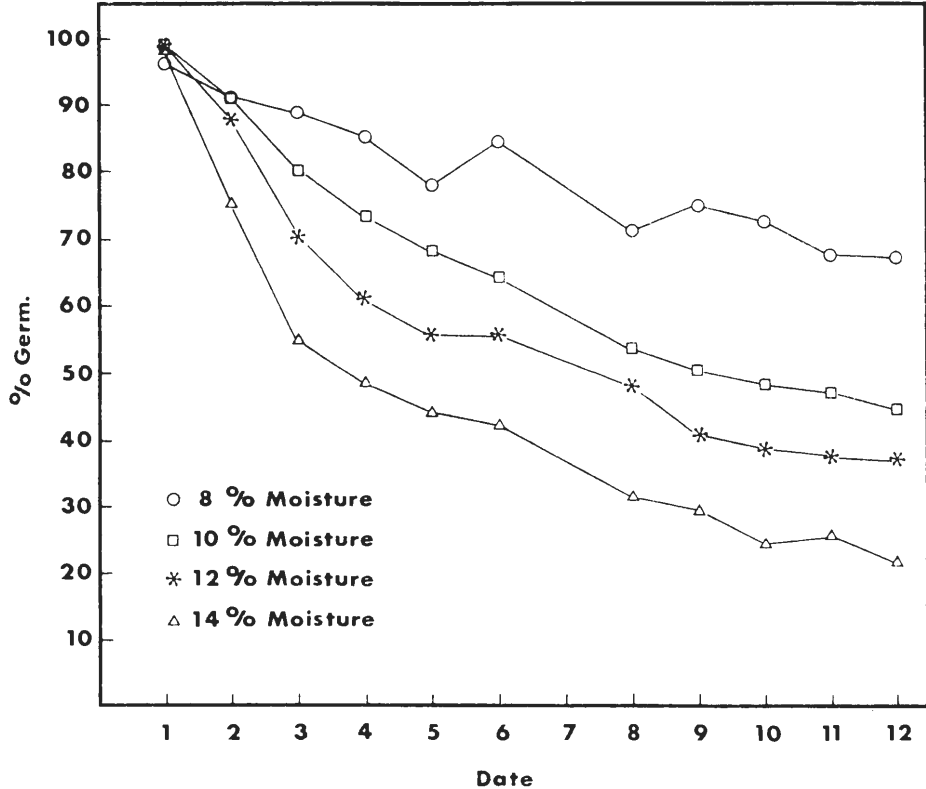


Figure 4. Effects of moisture content on germination percentage averaged across temperatures and varieties sampled at three-month intervals.

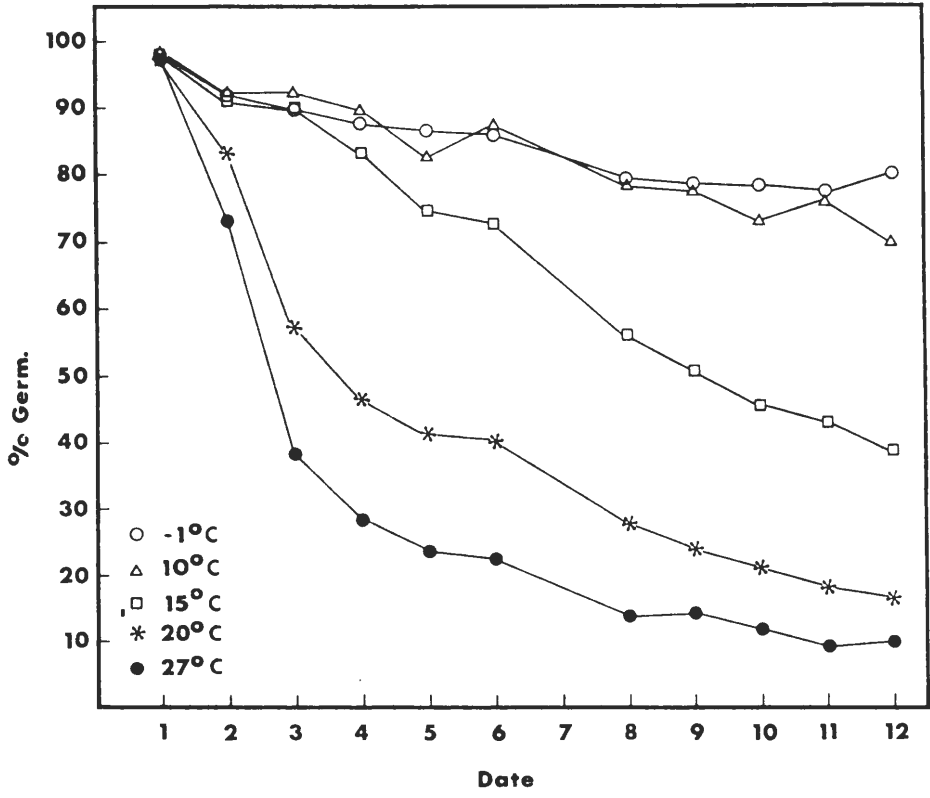


Figure 5. Effects of temperature on germination percentage averaged across moistures and varieties sampled at three-month intervals.

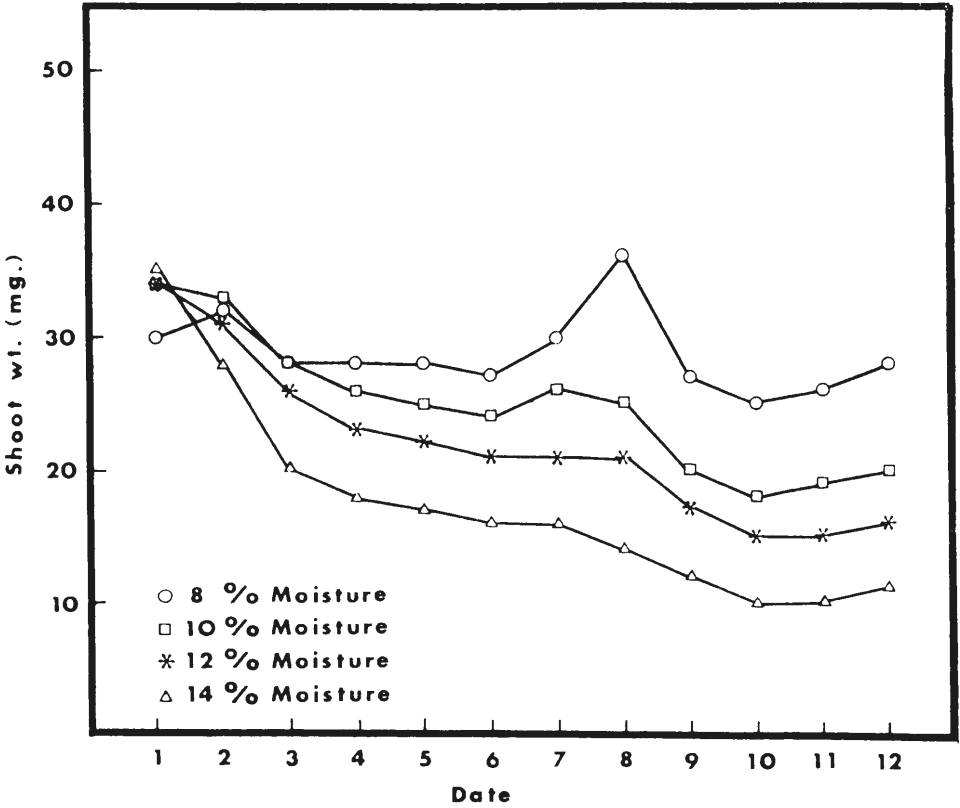


Figure 6. Effects of moisture on vigor (shoot weight) averaged across temperatures and varieties sampled at three-month intervals.

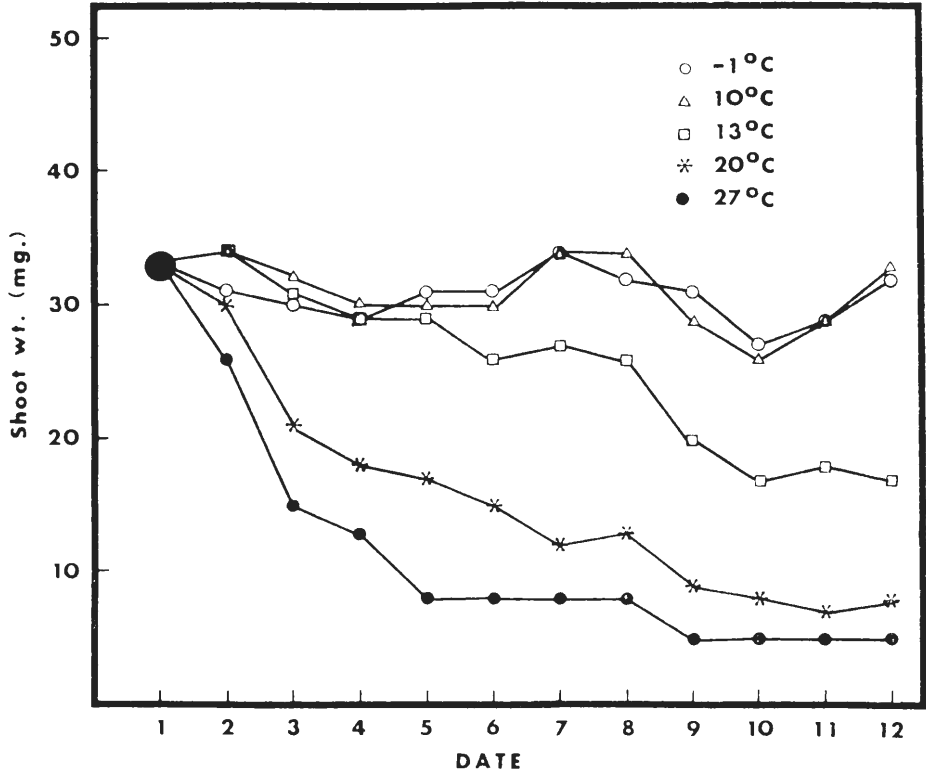


Figure 7. Effects of temperature on vigor (shoot weight) averaged across moistures and varieties sampled at three-month intervals.

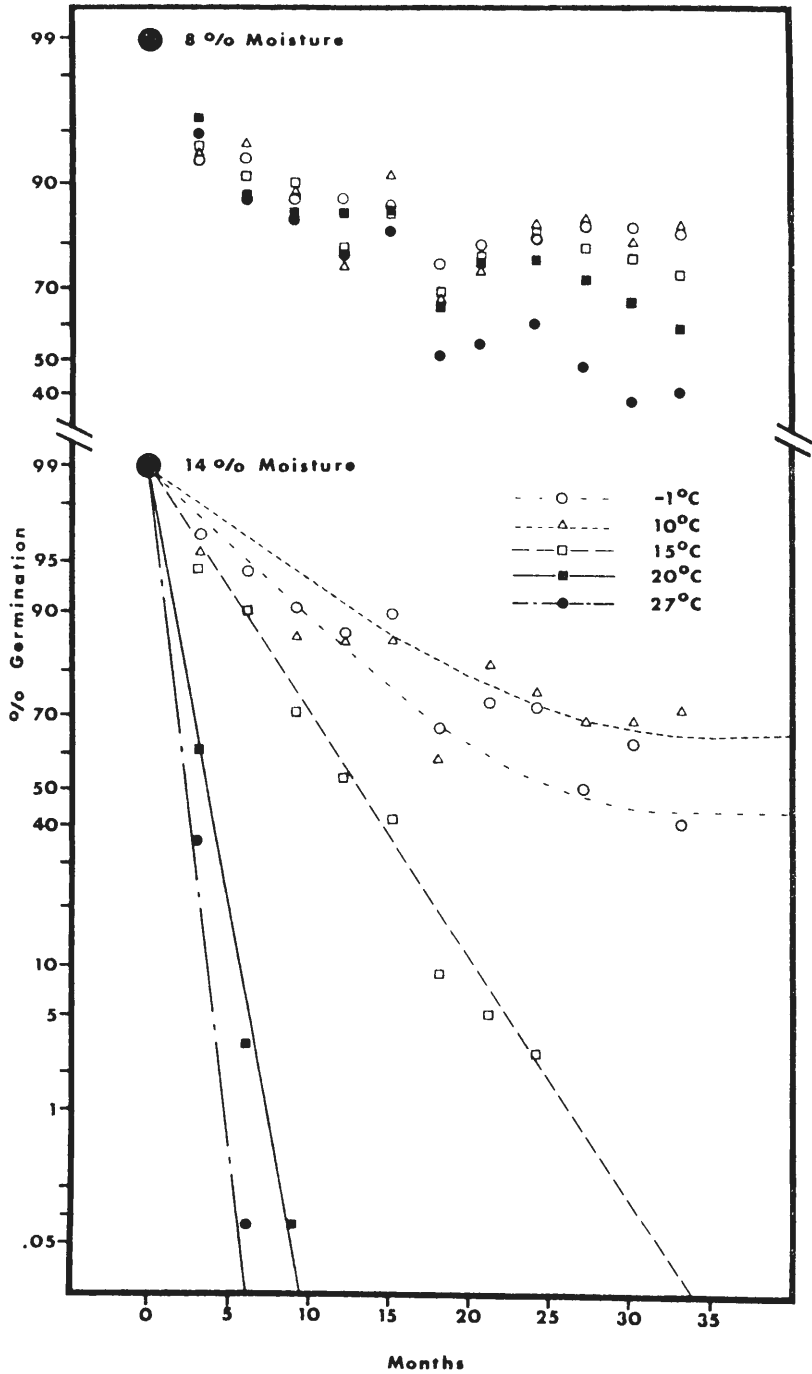


Figure 8. The percentage germination as effected by temperature, time in storage, and moisture content of the seed averaged across genotype on probability paper.

relationship may not be consistent with empirical storability. Further, using these constants, one can calculate a p_{50} for 8% moisture soybeans at 10 C of nearly ten years. The extended longevity predicted at the low moisture and temperatures may explain the apparent lack of normalcy in the germination responses. However, this does not justify the extrapolation of short-term, rapid-aging studies to long-term storage changes. In particular, it indicates the need for additional information comparing the physiological changes which occur under accelerated aging procedures with those changes that occur under normal storage conditions.

Aside from the confounding effect that the genotypic response may have on the predictive equations, they may provide a tool to improve storability. A breeding population cannot be efficiently screened through a one- or three-year storage study. But the apparent relationship between initial vigor, as measured by the shoot weight, and storability indicates that the vigor test provides a reasonably simple screening procedure. Additional data linking these two parameters would be beneficial, but the relationship in these experiments was consistent in both the one- and three-year studies. The general relationship then assumes that vigor and storability are both facets of the larger parameter "seed quality" and that, as such, are closely related.

The practical application of these results depends upon the storage options available to the seedsmen and the value of the seed to be stored. If mechanical manipulation of low moisture (8-10%) seed can be accomplished without significant seed damage, storage at these moisture levels should provide acceptable quality seed for at least three-five years. Small quantities of breeders or foundation seed can be handled individually, and their quality can easily be preserved. Larger volumes of seed are most efficiently preserved by reducing the temperature or moisture content of the environment. In a well-insulated warehouse, both moisture and temperature can be controlled at reasonable costs if necessary. However, reproduction of the seed on a one- or two-year cycle is probably a more energy-conserving alternative.

The practice of harvesting soybean seed at high (13.5%) moisture levels to reduce mechanical damage produces seed that has a single-season storage life. Thus, the seedsman, in effect, is determining the potential amount of carry-over seed that he will handle on the basis of moisture percentage of the seed at harvest or bagging. This management constraint can be eliminated if effective drying systems are available to reduce the moisture percentage to a safe level.

Thus, contrary to the current practice, the determination of lots to be carried over should be made on the basis of moisture content and initial quality during processing and not on the basis of a test done on remnant seed at the end of the planting season. This change in methods is justified by the magnitude of the moisture effect and the strong correlation between vigor and storability. Effective marketing would identify, at the processing step, those lots to be marketed first (high moisture and average vigor) and those that could be carried over (low moisture and high vigor).

Most previous studies have reported a decline in vigor prior to that of germination, which is not shown by the data herein. The time-relation of germination and vigor is, however, mediated by the method of vigor determination (Figures 6 and 7). If the dry weight of the seedlings produced by a seed sample is divided by the number of seed planted, and not by the number of seed that germinated normally, then vigor, so defined, decreases before germination. Both values offer insight into the aging process; it is presently not possible to assert that one is more correct than the other.

Changes in facets of seed quality during storage are best discussed in the context of their interrelationships. Temperature and moisture have separate and combined influences on both vigor and germinability. The confounding effect of genotype, although normally ignored, offers potential for improving storability through breeding. In addition, the predictive constants presented in foregoing text facilitate the practical management of seed storage. The causative agents involved in seed quality reductions during storage are not elucidated, but the magnitude of definition of these agents may be decreased because

of the evident relation between vigor and storability. The physical and physiological factors involved in soybean seed vigor are more manageable than three-year storage parameters.

LITERATURE CITED

- Association of Official Seed Analysts Seed Vigor Testing Committee. 1976. Assoc. Off. Seed Anal. Newsletter 50: 2.
- Byrd, H.W., and J.C. Delouche. 1971. Deterioration of soybean seed in storage. Proc. Assoc. Off. Seed Anal. 61: 41-48.
- Harrington, J.F. 1963. Practical advice and instructions on seed storage. Proc. Int. Seed Test. Assoc. 28: 989-994.
- Hukill, W.V. 1963. Storage of seeds. Proc. Int. Seed Test. Assoc. 28: 871-873.
- Roberts, E.H. 1960. The viability of cereal seed in relation to temperature and moisture. Ann. Bot. 24: 12-31.
- , 1972. Storage environment and the control of viability, pp. 14-58. In: E.H. Roberts (ed.). Viability of seeds. Syracuse Univ. Press. Syracuse, New York.
- Toole, E.H. and V.K. Toole. 1946. Relation of temperature and seed moisture to the viability of stored soybean seed. U.S. Dept. Agric. Circular 753. 9 pp.

RESISTANCE IN SUNFLOWERS TO SUNFLOWER MOTH¹

James L. Jarvis²

ABSTRACT. Sunflower introductions were evaluated in the field at Ames, Iowa, from 1975 through 1978 for resistance to the sunflower moth, *Homeosoma electellum*. Of the large-headed sunflowers evaluated, some 13 entries consistently had considerably lower sunflower moth infestation and damage than three commercial cultivars. Those with the least infestation and damage were PI 172906, PI 204578, and PI 380569. Infestation was somewhat less in small-headed, wild-type sunflowers than in those with large, single heads. Infestation and damage were lower in tall late-flowering introductions than in the short, early-flowering introductions.

INTRODUCTION

Sunflower, *Helianthus annuus* L., is becoming an increasingly important crop in the United States, and is surpassed only by soybeans as the leading oilseed crop in the world (Cobia and Zimmer, 1975). The sunflower moth, *Homeosoma electellum* (Hulst) is an important insect pest of the cultivated sunflower. Larvae infest the heads and cause extensive damage as they feed and tunnel in both the developing seeds and in the fleshy receptacle area. Infested heads are easily recognized because feeding by the larvae produces large amounts of frass, webbing, and damaged seeds.

The biology and oviposition habits of the sunflower moth are not well known. Satterthwait and Swain (1946) reported that the moth deposited eggs singly or in small masses among the sunflower florets. Carlson (1967) observed that the larvae, which hatch from eggs laid among disc flowers, bored into the developing seeds, and that webbing and frass appeared in peripheral areas of the heads soon after flowering. Teetes and Randolph (1969) demonstrated that sunflower moth oviposition is greatest on the third day after sunflower heads opened.

The effects of planting date on sunflower moth infestation have been studied by several researchers. In Nebraska, Muma et al. (1950) reported that sunflowers planted early (May 2) averaged fewer than one larva per head and that those planted late (June 8) averaged nearly three larvae per head. In Texas, however, Teetes and Randolph (1971) found the least infestation of sunflower moth larvae in plants planted either very early (March 12) or after April 17. In Georgia, Beckham and Tippins (1972) observed the heaviest sunflower moth infestations in sunflowers planted late. Seemingly, geographical location may determine the best planting date to lessen infestation.

Teetes et al. (1971) noted some differences in varietal resistance of sunflowers to the sunflower moth. Early-maturing Russian varieties and fast-flowering hybrids were least infested.

The studies reported here were conducted from 1975 through 1978 at the Plant Introduction Station, Ames, Iowa, to determine if certain sunflower introductions have natural resistance to the sunflower moth and to determine if sunflower moth infestation is related to specific plant characteristics.

¹Journal Paper No. J-9448 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa. Projects No. 1018 and 2135.

²Research Entomologist, Plant Introduction Research Unit, Agric. Res. SEA, Ames, Iowa 50011.

METHODS

The 1975 planting of sunflowers consisted of 78 accessions and was unreplicated. Two types were grown—plants with large heads, usually only one head per plant, and wild-type plants with from 5 to 40 heads per plant. Large-headed sunflowers were planted in the field on May 13. Wild multi-headed sunflowers were planted in the greenhouse May 14 and transplanted to the field June 1. At this time, the plants were nearly all the same size.

The 1976 planting consisted of 350 sunflower introductions planted on May 10 in a randomized complete block with three replications.

The 1977 planting, made on May 11, consisted of 60 sunflower introductions selected on the basis of their performance in 1976. Of these, 48 had shown promise in 1976 as possible sources of resistance to the sunflower moth and 12 were known to be susceptible. The experimental design used was a randomized complete block with four replications.

The 1978 planting consisted of the 13 sunflower introductions (listed in Table 1) that had the lowest level of infestations of any of those grown in 1977, plus three susceptible commercial cultivars. Two plantings were made in 1978, early (May 5) and late (May 22). Four replications were used for each planting date.

A natural infestation of sunflower moth developed in late July and August during each year of this study. Plants were examined for evidence of sunflower moth infestation and a system of visual ratings was used to estimate the degree of damage to infested heads. A rating of 1–3 was given for light damage, 4–6 for moderate damage, and 7–9 for severe damage. In 1977 and 1978, ten infested heads were selected at random from each plot and dissected, and the number of larvae were determined by count.

For each accession the average head diameter and plant height and the days from planting to midflowering were recorded to determine if a relationship existed between these plant traits and sunflower moth infestation.

RESULTS

In 1975 sunflower moth infestation was fairly uniform over the entire planting; 60% of the heads were infested, and the average damage rating was 5.9. About one-third of the total seed production was lost because of sunflower moth infestation. Only one accession, PI 204578 from Turkey, showed promise as a source of resistance to sunflower moth.

In 1976 the entire sunflower collection, consisting of 350 accessions, was evaluated. Infestation by sunflower moth was moderately heavy; 53% of the heads were infested, and the average damage rating for infested heads was 5.8. As in the previous year, approximately one-third of the seed was lost. Of the 350 sunflower introductions grown, 48 had 10% or less of their heads infested by sunflower moth. Presumably most of these were resistant to sunflower moth or were possibly unattractive to ovipositing adults. Introductions PI 172906, PI 204578, and PI 380569 had no infestation.

In 1977 the 48 introductions that seemed resistant in 1976 were grown again, along with 12 introductions that were known to be susceptible. Sunflower moth infestation was very heavy (possibly because of the extreme drought) and fairly uniform; 83% of the heads were infested, and the average damage rating was 6.3. Seed loss was estimated to be 60% of the total production. The susceptible entries previously rated had 99% of their heads infested; those entered as resistant (10% or less infestation in 1976) had 78% of the heads infested.

Table 1 lists sunflower introductions that had a damage rating of less than 5.0 in 1977 along with three susceptible commercial cultivars. Introductions are listed in ascending order of percent infested heads. This table also relates levels of sunflower moth infestation to specified plant characteristics.

The 1977 entries were again planted in 1978, this time at two dates, May 5 and May 22. The 1978 data verified the comparative resistance of the most promising introduc-

Table 1. Sunflower introductions with a damage rating of less than 5, Ames, Iowa, 1977.

Plant Introduction Number or Cultivar	Source of original seed	No. plants examined	Percent infested heads	Head diameter, cm	Plant height, cm	Days to mid- flowering	Average damage rating	Average no. larvae per infested head
380569	Kenya	20	0	23	350	98	0	0
204578	Turkey	56	11	15	170	90	1.8	0.7
172906	Turkey	48	12	23	300	63	2.6	1.6
171657	Turkey	30	33	24	225	91	3.5	3.3
171656	Turkey	38	42	23	278	81	4.1	5.7
369357	Indiana	28	57	19	255	72	4.4	2.2
176974	Turkey	54	66	18	270	90	4.4	4.6
369358	Indiana	37	70	24	220	71	4.0	5.7
226466	Iran	35	89	28	225	44	4.6	3.4
380563	Kenya	20	90	25	238	78	3.7	1.9
343809	Iran	32	91	20	205	78	3.1	1.2
162453	Uruguay	38	92	28	218	72	4.5	5.2
380562	Kenya	23	100	24	250	85	4.8	4.1
Arrowhead	USA	40	100	19	155	59	7.8	21.4
Mennonite	USA	37	100	17	150	65	7.5	18.1
Mingren	USA	46	100	20	150	67	6.8	14.8

Table 2. Effect of planting date of selected sunflower introductions on sunflower moth infestation, Ames, Iowa, 1978.

Plant Introduction Number or Cultivar	Early Planting (May 5)				Late Planting (May 22)		
	Source of original seed	Percent infested heads	Average damage rating	Average no. larvae per infested head	Percent infested heads	Average damage rating	Average no. larvae per infested head
204578	Turkey	0	—	—	0	—	— ^a
380569	Kenya	0	—	—	0	—	—
172906	Turkey	5	1.0	1.5	0	—	—
369357	Indiana	10	3.7	3.0	0	—	—
176974	Turkey	13	3.7	2.9	0	—	—
171657	Turkey	20	3.0	3.1	0	—	—
171656	Turkey	23	3.9	3.0	3	2.5	2.0
380563	Kenya	23	5.8	5.4	3	3.0	2.0
369358	Indiana	28	5.0	4.0	18	4.7	3.5
380562	Kenya	35	4.8	4.2	8	2.7	1.5
Mingren	USA	38	5.6	4.8	23	2.6	2.5
Mennonite	USA	45	5.9	7.0	35	6.3	5.3
343809	Iran	53	4.5	3.8	30	4.1	3.0
Arrowhead	USA	58	6.5	10.1	38	6.7	5.1
162453	Uruguay	60	4.2	5.1	30	4.1	3.1
226466	Iran	70	6.1	7.5	43	5.3	4.0

^aDashes in this and subsequent tables means no observations were made.

Table 3. Relation between head diameter of sunflowers and sunflower moth infestation, Ames, Iowa, 1975-1977.

Average head diameter (cm)	Number of accessions	Number of plants	Percent infested heads	Average damage rating	Average number of larvae per infested head
1975 infestation					
1-4	43	353	43	6.2	No data
5-7	5	55	48	7.2	
8-10	0	—	—	—	
11-13	7	49	83	6.5	
14-16	4	40	90	6.0	
17-19	1	10	100	8.0	
20-22	9	90	84	5.5	
23-25	6	60	85	5.2	
26-28	3	30	97	7.0	
1976 infestation					
8-10	1	20	5	6.0	No data
11-13	3	6	33	8.0	
14-16	19	297	69	6.3	
17-19	61	985	49	5.6	
20-22	101	1402	60	5.3	
23-25	91	1099	51	4.9	
26-28	56	509	49	4.9	
29-31	15	140	70	5.3	
32-34	3	22	54	5.7	
35-37	1	10	30	3.0	
1977 infestation					
8-10	1	57	51	6.3	5.8
11-13	1	50	90	5.6	5.2
14-16	1	56	11	1.8	0.7
17-19	7	279	77	6.2	9.8
20-22	8	234	93	6.5	14.6
23-25	25	918	79	5.9	12.9
26-28	14	518	97	6.8	16.4
29-31	2	74	100	8.2	19.1
32-35	1	38	100	7.7	16.7

Table 4. Relation between days to midflowering of sunflowers and sunflower moth infestation, Ames, Iowa, 1975-77.

Days to mid-flowering	Number of accessions	Number of plants	Percent infested heads	Average damage rating	Average number of larvae per infested head
1975 infestation					
60-64	8	62	90	6.4	No data
65-69	15	147	88	8.5	
70-74	12	133	64	6.7	
75-79	12	98	48	6.9	
80-84	10	100	67	4.7	
85-89	10	89	36	5.8	
90-94	4	23	8	4.3	
95-99	7	35	32	4.3	
1976 infestation					
35-39	2	22	91	8.5	No data
40-44	10	147	88	6.5	
45-49	30	566	71	6.5	
50-54	25	419	57	5.4	
55-59	40	349	58	5.7	
60-64	62	659	58	5.1	
65-69	69	876	60	5.4	
70-74	41	536	47	4.7	
75-79	22	298	46	5.0	
80-84	19	379	26	3.4	
85-89	15	190	29	3.4	
90-94	12	119	23	3.1	
95-99	1	5	0	—	
100-104	2	25	0	—	
1977 infestation					
40-44	1	35	88	4.6	9.3
45-49	0	—	—	—	—
50-54	2	63	100	7.3	16.1
55-59	5	197	98	7.0	12.0
60-64	5	189	75	6.4	12.9
65-69	10	370	91	7.5	16.3
70-74	10	398	89	6.6	4.0
75-79	5	171	94	5.2	3.9
80-84	11	401	80	6.6	7.2
85-89	5	145	90	6.1	8.5
90-94	5	235	53	4.6	5.2
95-99	1	20	0	—	—

Table 5. Relation between height of sunflowers and sunflower moth infestation, Ames, Iowa, 1976-77.

Average plant height (cm)	Number of accessions	Number of plants	Percent infested heads	Average damage rating	Average number of larvae per infested head
1976 infestation					
76-100	1	7	71	8.0	No data
101-125	8	70	56	5.2	
126-150	39	373	69	5.9	
151-175	67	951	55	6.2	
176-200	124	1666	57	5.4	
201-225	58	750	46	4.6	
226-250	23	278	35	4.3	
251-275	18	251	23	3.1	
276-300	7	90	11	2.1	
301-325	1	15	0	—	
326-350	4	29	34	3.0	
1977 infestation					
101-125	1	39	100	8.0	21.2
126-150	5	189	97	7.3	17.9
151-175	7	282	82	6.7	16.5
176-200	14	505	91	7.3	14.1
201-225	15	523	84	5.8	8.4
226-250	8	294	86	6.1	11.6
251-275	6	286	84	5.5	6.0
276-300	2	86	26	3.3	2.5
301-325	1	20	45	5.0	7.1
326-350	1	20	0	—	—

Table 6. Correlation coefficients between plant characteristics and sunflower moth infestation, Ames, Iowa, 1975-77.

Variables correlated	Correlation coefficient
1975 infestation	
Percent infestation and head diameter	0.720**
Percent infestation and days to midflowering	-0.247*
Percent infestation and damage rating	.599**
1976 infestation	
Percent infestation and head diameter	-0.007
Percent infestation and days to midflowering	-0.400**
Percent infestation and plant height	-0.341**
Percent infestation and damage rating	.634**
1977 infestation	
Percent infestation and head diameter	.269*
Percent infestation and days to midflowering	-0.441**
Percent infestation and plant height	-0.554**
Percent infestation and damage rating	.816**
Larvae per infested head and head diameter	.282*
Larvae per infested head and days to midflowering	-0.318*
Larvae per infested head and plant height	-0.513**
Larvae per infested head and damage rating	.850**
Larvae per infested head and percent infestation	.714**

* Significant at the 5% level of probability.

** Significant at the 1% level of probability.

There are 76 degrees of freedom for the 1975 correlations, 348 degrees of freedom for the 1976 correlations, and 61 degrees of freedom for the 1977 correlations.

tions (Table 2), and all except three of the entries had a lower infestation than the commercial cultivars. Sunflower moth infestation, however, was less in 1978 than in any other year of this study.

Time of planting affected infestation. Among the resistant introductions, in the early planting, 26% of the heads were infested, while in the late planting, only 10% of the heads were infested. Comparable values were 47% and 32% for the susceptible commercial cultivars.

The introductions PI 172906, PI 204578, and PI 380569 seem most promising for resistance to the sunflower moth. Of these, the most unusual is PI 204578, an ornamental sunflower from Turkey. The head of a typical sunflower has a black center ringed with yellow petals (ligulate flowers). The head of PI 204578, however, has only long, yellow, ligulate flowers and resembles a gigantic chrysanthemum. This introduction should be further investigated.

Table 3 shows the relationship between head diameter of sunflowers and sunflower moth infestation. In 1975, wild-type, multiheaded sunflowers, which have head diameters of 10 cm or less, had less than 50% of their heads infested; accessions with larger single heads had 83-100% infestation. The relationship between head diameter and infestation was not distinctive for accessions having head diameters greater than 10 cm.

Table 4 shows the relationship between days from planting to mid-flowering and

sunflower moth infestation. In all years (1975, 1976, 1977, 1978), late-flowering introductions had a lower percentage of the heads infested, lower damage ratings, and fewer sunflower moth larvae per infested head than did early-flowering introductions.

Table 5 shows the relation between plant height and sunflower moth infestation. Taller accessions tended to have a lower percentage of infested heads, lower damage ratings, and fewer larvae per infested head than did shorter accessions.

Correlation coefficients were computed to identify any statistically significant relation between plant characteristics and indices of sunflower moth infestation, (Table 6). For the statistical analysis, the percentages were transformed to arcsine values.

The correlation between percentage sunflower moth infestation and head diameter was significant at the 1% level in 1975, nonsignificant in 1976, and significant at the 5% level in 1977. The correlation between these two variables was higher in 1975 because many of the sunflowers grown were wild, small, multiheaded types, which had less infestation than large, single-headed plants grown in 1976 and 1977. In 1975, the negative correlation between percentage sunflower moth infestation and days to mid-flowering was significant at the 5% level; in 1976 and 1977, these correlations were significant at the 1% level. Also in 1977, the correlation between numbers of sunflower moth larvae per infested head and days to midflowering was significant at the 1% level. Thus, sunflower moth infestations were significantly greater in early-flowering sunflower introductions than in late-flowering introductions.

The negative correlation between percentage sunflower moth infestation and plant height was significant at the 1% level in 1976 and 1977; the correlation between larvae per infested head and plant height was significant at the 1% level in 1977. Thus, sunflower moth infestation was significantly greater in sunflower introductions with shorter stalks than in the taller introductions.

The correlations between percentage sunflower moth infestation and damage ratings were significant at the 1% level of probability in 1975, 1976, and 1977. The correlations between numbers of larvae per infested head and both damage ratings and percentage infestation were highly significant. Thus, differences in sunflower moth infestation and damage among sunflower introductions may be due to attractiveness of sunflowers to ovipositing moths.

It is, therefore, evident that sunflower moth infestation is greatest in short, early-flowering sunflower introductions. These introductions are probably more heavily infested because sunflower moth adults are active when early-maturing sunflowers are in bloom. Adults are known to deposit their eggs on flowers soon after the heads open and while the flowers are in bloom (Teetes and Randolph, 1969).

Early planting of sunflowers resulted in reduced populations of sunflower moth in Nebraska (Muma et al., 1950) and in Georgia (Beckham and Tippins, 1972). In Texas, populations of sunflower moth were lower when sunflowers were planted either very early or late (Teetes and Randolph, 1969, 1971). Studies conducted from 1975 through 1978 indicate that, in the Ames area (central Iowa), delaying planting or planting late-flowering sunflowers will significantly reduce sunflower moth infestation. This, however, may not be true elsewhere, and consequently the best time to plant sunflowers to minimize sunflower moth infestation may vary according to geographical location.

LITERATURE CITED

- Beckham, C.M., and H.H. Tippins. 1972. Observations of sunflower insects. *J. Econ. Ent.* 65: 865-866.
- Carlson, E.C. 1967. Control of sunflower moth larvae and their damage to sunflower seeds. *J. Econ. Ent.* 60: 1068-1071.
- Cobia, D., and D. Zimmer. 1975. Sunflowers: production, pests, and marketing. North Dakota State Univ. Coop. Ext. Serv. Bull. 25. 59 pp.

- Muma, M.H., R.N. Lyness, C.E. Claasen, and A. Hoffman. 1950. Control tests on sunflower insects in Nebraska. *J. Econ. Ent.* 43: 477-480.
- Satterthwait, A.F., and R.B. Swain. 1946. The sunflower moth and some of its natural enemies. *J. Econ. Ent.* 39: 575-580.
- Teetes, G.L., M.L. Kinman, and N.M. Randolph. 1971. Differences in susceptibility of certain sunflower varieties and hybrids to the sunflower moth. *J. Econ. Ent.* 64: 1285-1287.
- , and N.M. Randolph. 1969. Chemical and cultural control of the sunflower moth in Texas. *J. Econ. Ent.* 62: 1444-1447.
- , -----, 1971. Effects of pesticides and dates of planting sunflowers on the sunflower moth. *J. Econ. Ent.* 64: 124-126.

QUATERNARY STRATIGRAPHY OF THE LOWER PART OF PIONEER
CREEK BASIN, CEDAR AND JONES COUNTIES, IOWA

John P. Szabo¹

ABSTRACT. Several borehole traverses were made across the classic Kansan areas, paha, and the Iowa Erosion Surface in the lower part of Pioneer Creek Basin in Cedar and Jones Counties, Iowa. These traverses along with radiocarbon dates established the stratigraphy of the area. In the paha Wisconsinan, loess and eolian sand overlie a Late-Sangamon paleosol developed in the uppermost till. The lower part of this till is interbedded with or overlies fluvial deposits, which, in turn, overlie a lower till unit. On the Iowan area the paleosol and part of the upper till are truncated by the erosion surface, exposing the lower part of the upper till and the fluvial sediments. The upper till is correlated with the Pre-Illinoian Hickory Hills Till Member of the Wolf Creek Formation, and the lower till correlates with the Alburnett Formation. Physical stratigraphy and radiocarbon dates show that fluvial silts, sands, and peat in the valley are of Late-Wisconsinan age and contemporaneous with loess deposition and development of the erosion surface.

INTRODUCTION

Reconnaissance borings in valleys in east-central Iowa from 1969 through 1973 showed that sediments (colluvium, alluvium, eolian sands, peat and lacustrine silts) overlie classic Kansas till and underlie or interfinger with Late Wisconsinan loess. It seemed possible that these sediments might span the little-known interval, Illinoian through Late Wisconsinan, in east-central Iowa. In order to verify this possibility, a field area encompassing 70 km² was chosen around the lower part of Pioneer Creek basin near Mechanicsville, Iowa, in the northwestern corner of Cedar County and the southwestern corner of Jones County (Fig. 1). The site includes parts of T. 82 N., R. 3 W. and T. 83 N., R. 3 W. in the Mechanicsville and Stanwood quadrangles (1:24,000).

The field area contains four topographic divisions. The eastern and northern part of the field area (Fig. 2) displays the topography characteristic of the "Iowan till plain" (Norton, 1901), now known as the Iowan Erosion Surface (Ruhe, 1968). The gently undulating surface is slightly dissected with an average relief of nearly six meters. The Kansan area to the southwest is more dissected than the Iowan (Fig. 2). Many loess-capped elongated interfluves give the Kansan area greater relief than the Iowan area. The tributaries to Pioneer Creek have narrower and deeper valleys than those of the Iowan. The Stanwood Paha (Fig. 2) trends northwest-southeast between the Iowan and Kansan and shows topography characteristic of the Kansan. The paha tapers into the Iowan topography at its southeastern end, but its northwestern end merges into the adjacent Kansan landscape. Pioneer Creek is an underfit stream in the field area (Fig. 2). Several small hills which were significant to the stratigraphy protrude from the flood plain in section 5 (Fig. 2).

This area was examined in the late nineteenth and early twentieth centuries. McGee (1891) named the largest paha in the area the "Stanwood paha," and discovered two tills which he mapped as "upper till" and "lower till." Chamberlin (1895) named McGee's upper till, "Iowan," and his lower one, "Kansan." Calvin (1896) and Norton (1901), on the other hand, could not discriminate between the Iowan and Kansan tills, and Alden and Leighton (1917) stated that they were similar.

¹Department of Geology, University of Akron, Akron, Ohio.

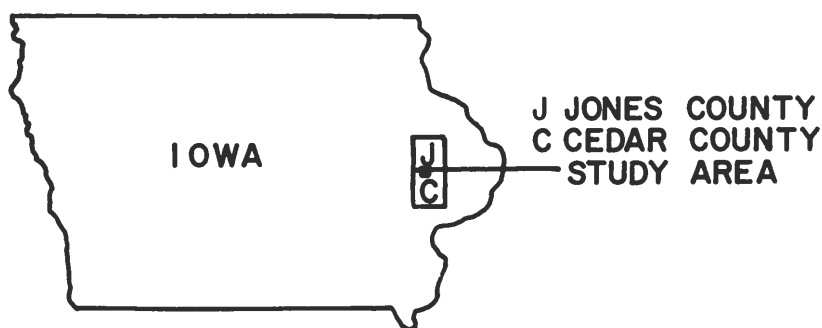


Figure 1. Location of study area.

Because early geologists could not distinguish between the Iowan and Kansan tills in the field area (Fig. 3), the apparent mixing of Iowan and Kansan topographic characteristics near Mechanicsville caused disagreement. The fact that Scholtes and Smith (1950) studied the soils of the paha, which are more characteristic of the classic Kansan, may account for their interpretation of the Iowan-Kansan boundary. However, Norton (1901) and the Iowa Geological Survey (1917, 1955) regarded many of the paha in the Mechanicsville area as inliers of Kansan till. Ruhe *et al* (1968) established that the Iowan till did not exist and that the Iowan is an extensive erosion surface. Ruhe (1969) considered the paha as loess-covered erosional remnants of a Yarmouth-Sangamon surface on Kansan till. Miller (1974) extended the Iowan Erosion Surface beyond the classical boundary. Also, the Soil Conservation Service (1974) completed field maps of Cedar County that provided insight into the distribution of Quaternary materials on the surface of the field area. The history of the Iowan has been reviewed recently by Hallberg *et al* (1978b).

METHODOLOGY

Because few outcrops exhibited more than a single stratigraphic unit, 157 boreholes were drilled along several traverses from the valley of Pioneer Creek onto the Iowan surface, onto the Kansan upland, and onto the Stanwood paha (Szabo, 1975). Some holes were drilled by using a Belgian auger or a bucket auger. A Giddings soil probe was used for coring and continuous flight augering. Cores were described and sampled in the laboratory; auger sections were described and sampled in the field. Borehole data from these traverses were used to establish the relative age of the deposits.

In the laboratory, paleosols were described to aid in the interpretation of the geologic history of the area. Textural analyses were performed on the samples following the procedure of Folk (1965). The clay mineralogy was determined by x-ray diffraction following the procedure of H. Glass of the Illinois State Geological Survey (Hallberg *et al*, 1978c). Two other measures were recorded from the x-ray diffractograms of each sample. The diffraction intensity (DI), a ratio of counts of illite (10 Å) to counts of kaolinite and chlorite (7.2 Å) (Frye *et al*, 1962), was calculated. Also the heterogeneous swelling index (HSI), the height in mm of the expandable clay mineral peak (17 Å) (Willman, *et al*, 1966), was measured.

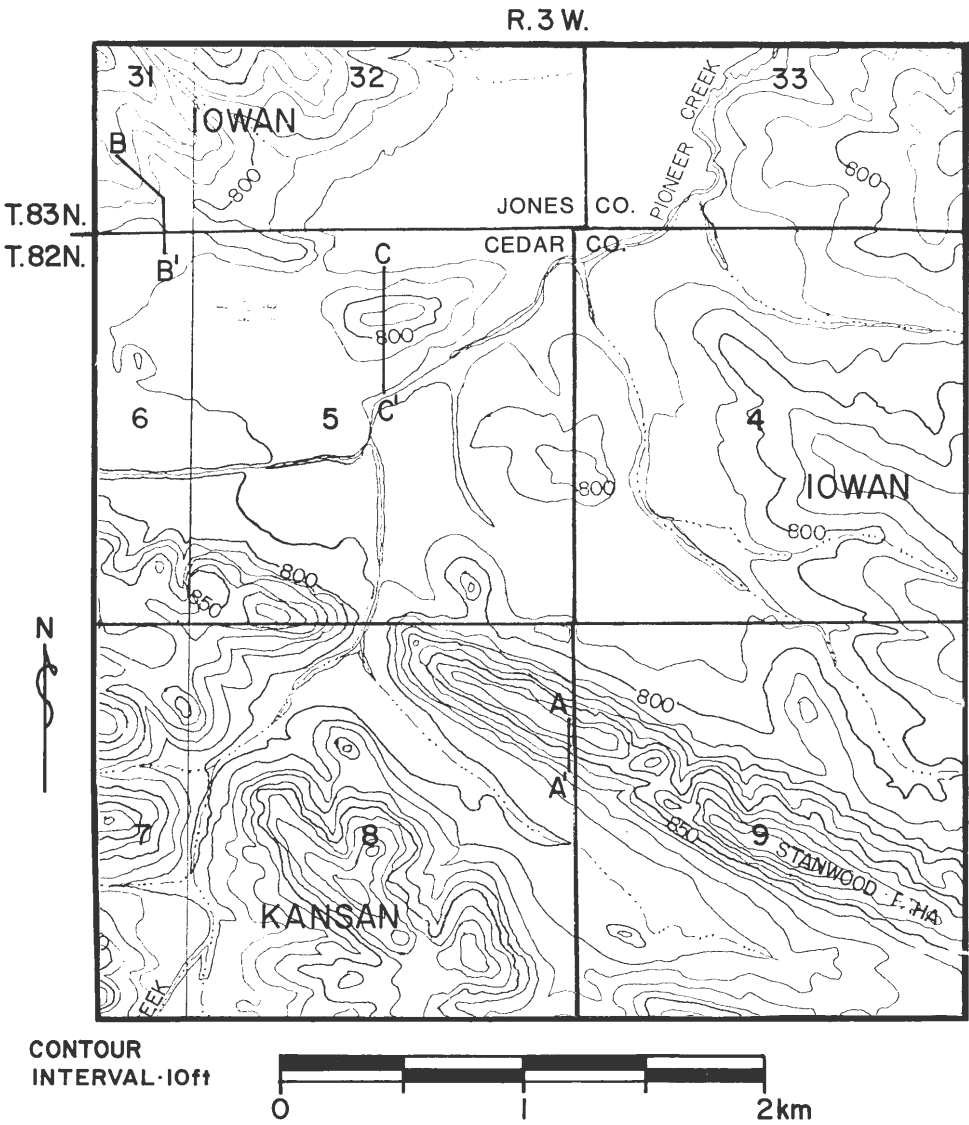


Figure 2. Topographic map of part of the study area, showing borehold traverses: A-A', B-B', and C-C'.

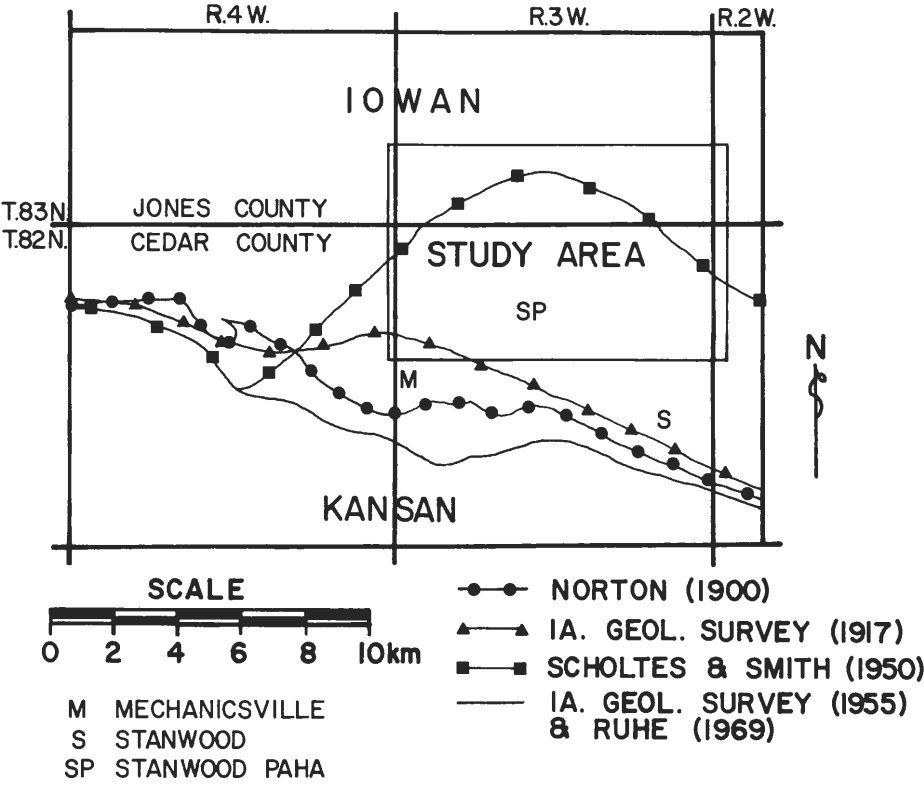


Figure 3. Various Iowan-Kansan boundaries.

STRATIGRAPHY

Paha

The Stanwood Paha in the field area is similar to those of Ruhe (1965) and Miller (1974). The stratigraphy of the paha is characteristic of the Kansan area (Ruhe, 1969). Loess overlies the upper till in the crest of the paha and overlies medium to coarse sands along the flanks of the paha (Fig. 4). A sand zone, separating the loess into two units, is composed of eolian sand or interbedded loess and eolian sand. This zone rests on the upper till on the northern side of the crest of the paha (Fig. 4); but farther north and down-slope on the flank of the paha, this zone is underlain by a lower unit of loess (Fig. 4). A sand zone is found on the southern flank of the paha, but it is not traceable onto the crest in this traverse.

The loess, itself, may be divided into several zones (Fig. 4) based on oxidation and leaching (Hallberg *et al.*, 1978d). The organic zone at the base of the loess or basal loess paleosol (Hallberg *et al.*, 1978b) is traceable for only 61 m on the crest of the paha. The zone is .3 to .6 m thick, dark-gray, partly leached, and contains flecks of carbon.

The loess is underlain by either a reddish-brown paleosol or by a dark greenish-gray paleosol. These paleosols are found in the upper till in several boreholes in the crest of the paha (Fig. 4).

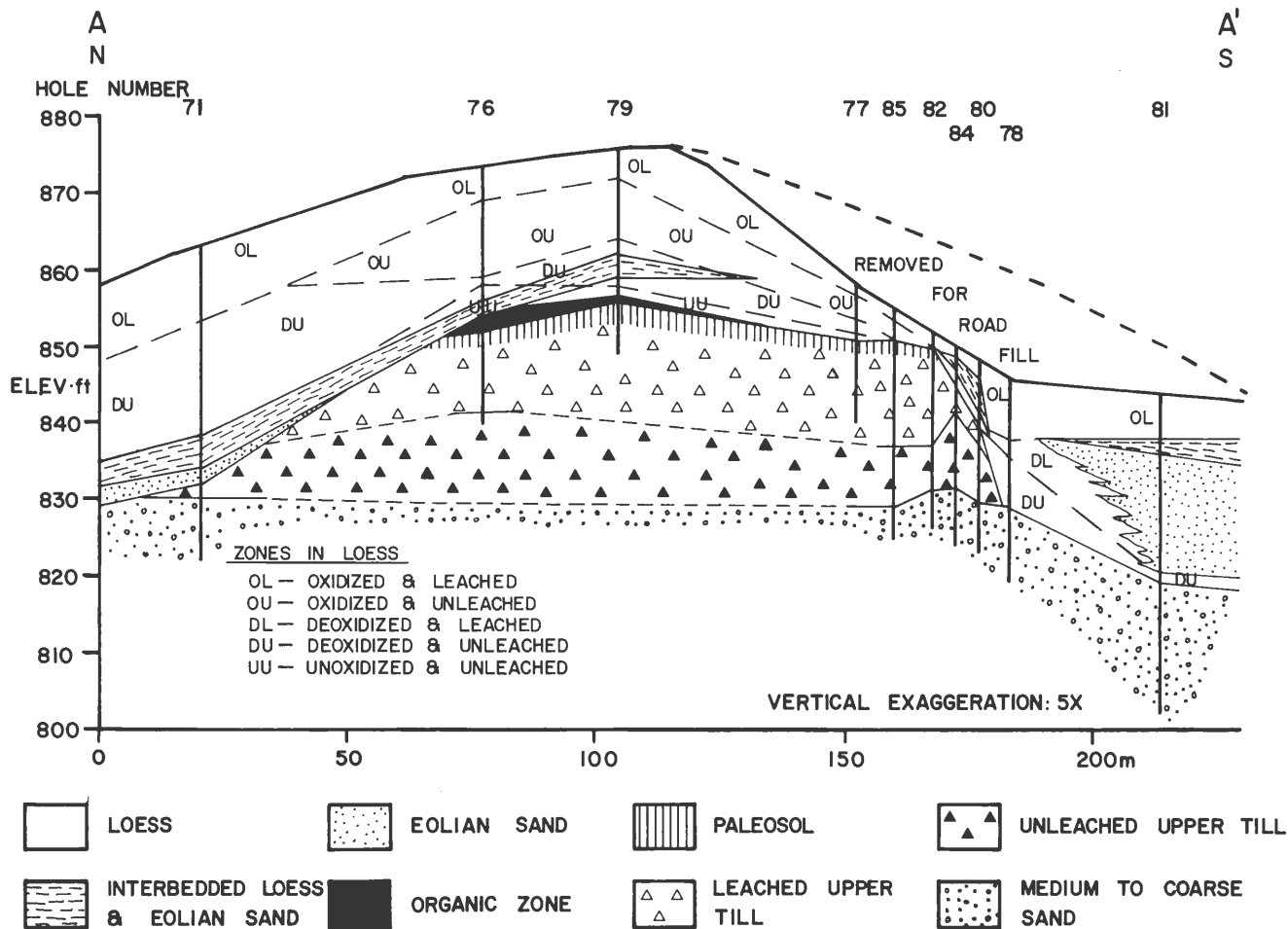


Figure 4. Cross section through the crest of the Stanwood paha along traverse A-A' (Fig.2)

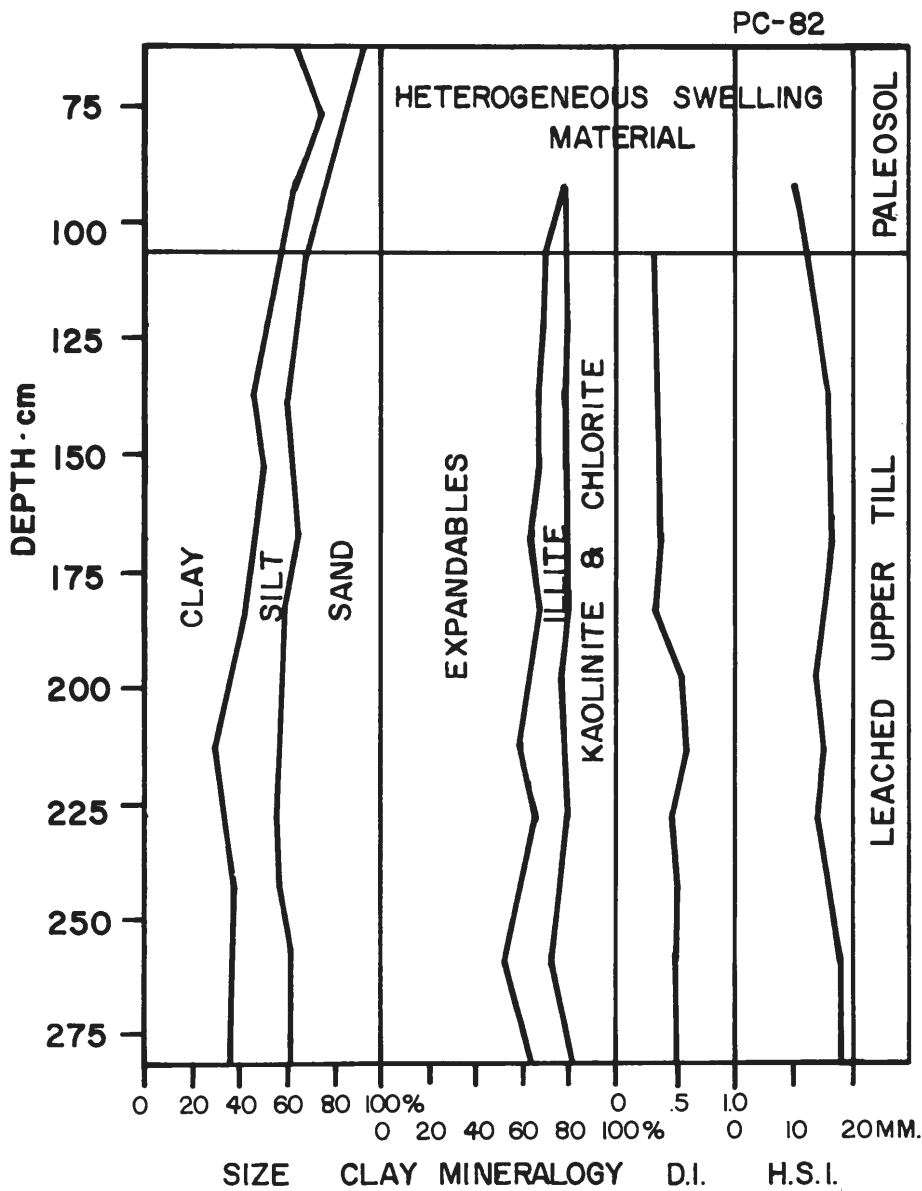


Figure 5. Laboratory analyses of the paleosol in hole 82 on traverse A-A' (Fig. 4).

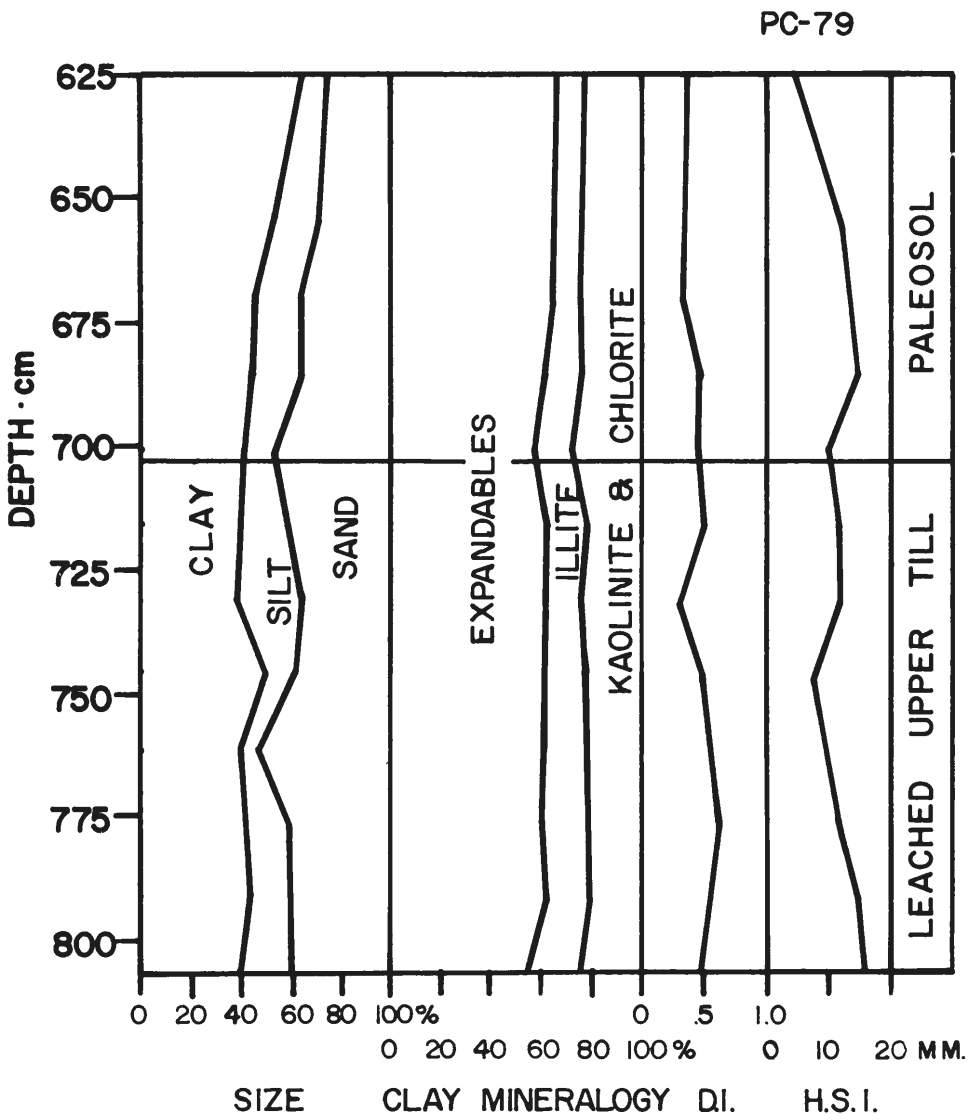


Figure 6. Laboratory analyses of the paleosol in hole 79 on traverse A-A' (Fig. 4).

The reddish-brown paleosol in hole 82 has the characteristics of a well-drained soil (Willman *et al.*, 1966). It is buried by .6 m of loess (Fig. 4); its reddish-brown, granular upper part contains 60 to 70 percent clay (Fig. 5), and is a truncated B-horizon. The paleosol grades into yellowish-brown, leached upper till. Figure 5 shows how the DI decreases near the top of the paleosol. The 17 Å peak is so broad and flat that the amount of expandables, the DI, and the HSI cannot be measured.

The dark greenish-gray paleosol in hole 79 on the crest of the paha (Fig. 4) is very firm and structureless. It has a sharp contact with yellowish-brown, leached upper till and has sharp x-ray diffraction peaks which allow the amounts of clay minerals, the DI, and the HSI to be calculated (Fig. 6).

Medium to coarse sands underlie the upper till in the crest of the paha. The upper part of these sands consists of fine sand, resembling eolian sand. Along the flanks of the paha, it is impossible to visually distinguish between the sand zone in the loess and the upper part of the sand unit which emerges under the loess where the upper till and paleosol are truncated by the erosion surface. Data from textural analyses support this contention (Szabo, 1975).

Section 31 Interfluv

The cross-section (Fig. 7) of the interfluv illustrates the relationship of the upper till in the Iowan area to the Silurian bedrock and to the lower fluvial silts and sands, and also shows the irregularities of the loess thickness. A sand zone is found in the loess farther downslope. The loess on the nose of the interfluv is like that of the Kansan area and the paha while the loess where the interfluv connects to the upland is like that of the Iowan area. Seven and one-half to 12.5 cm of reddish-brown, sticky, clayey loam identified as pedisegment is found at the base of the loess in holes 93, 94, and 95 (Fig. 7). The loess directly above the pedisegment is also reddish-brown; this suggests that part of the loess was derived from pedisegment or heavily oxidized till upslope.

The upper till is thin over the Silurian bedrock in the crest of the interfluv and wedges out over the lower fluvial silts and sands to the southeast (Fig. 7). At its base, the till is interbedded with coarse sand.

A complex paleosol is developed in the lower fluvial silts and sands (Fig. 7). It is very firm and gray with sandy layers and occasional pebbles, resembles an accretion-gley, and is traceable under the upper till. In hole 87 (Fig. 7), the upper 3 m of the paleosol contains small, blocky peds with thick clay skins.

A well-drained soil profile may be superimposed on an older accretion-gley on the interfluv. The upper 30 cm of the paleosol (Fig. 8) may be mixed with the overlying loess. Although the paleosol's upper part contains 50 to 60 percent clay, no strong textural B-horizon is indicated. The clay may be relict from the gleying process. Heterogeneous swelling material in the upper .9 m of the paleosol (Fig. 8) indicates the formation of a B-horizon. The clay mineralogy is similar to that of the lower fluvial silts and sands 6.1 m below the paleosol (Szabo, 1975). Laboratory analyses and stratigraphy imply that the well-drained part of the paleosol should be younger than the upper till but older than the loess.

The lower fluvial silts and sands below the paleosol are heavily mottled and leached. The lower part of the lower fluvial sequence grades into coarse sands and gravels (Fig. 7) and contains small wood fragments. No boreholes were deep enough to penetrate the lower till in this part of the field area.

Section 5 Hill

The hill in the N 1/2 sec. 5, T. 82 N., R. 3 W (Fig. 3) is significant in two ways. First, the characteristics of the classic Iowan and Kansan areas are blended together in

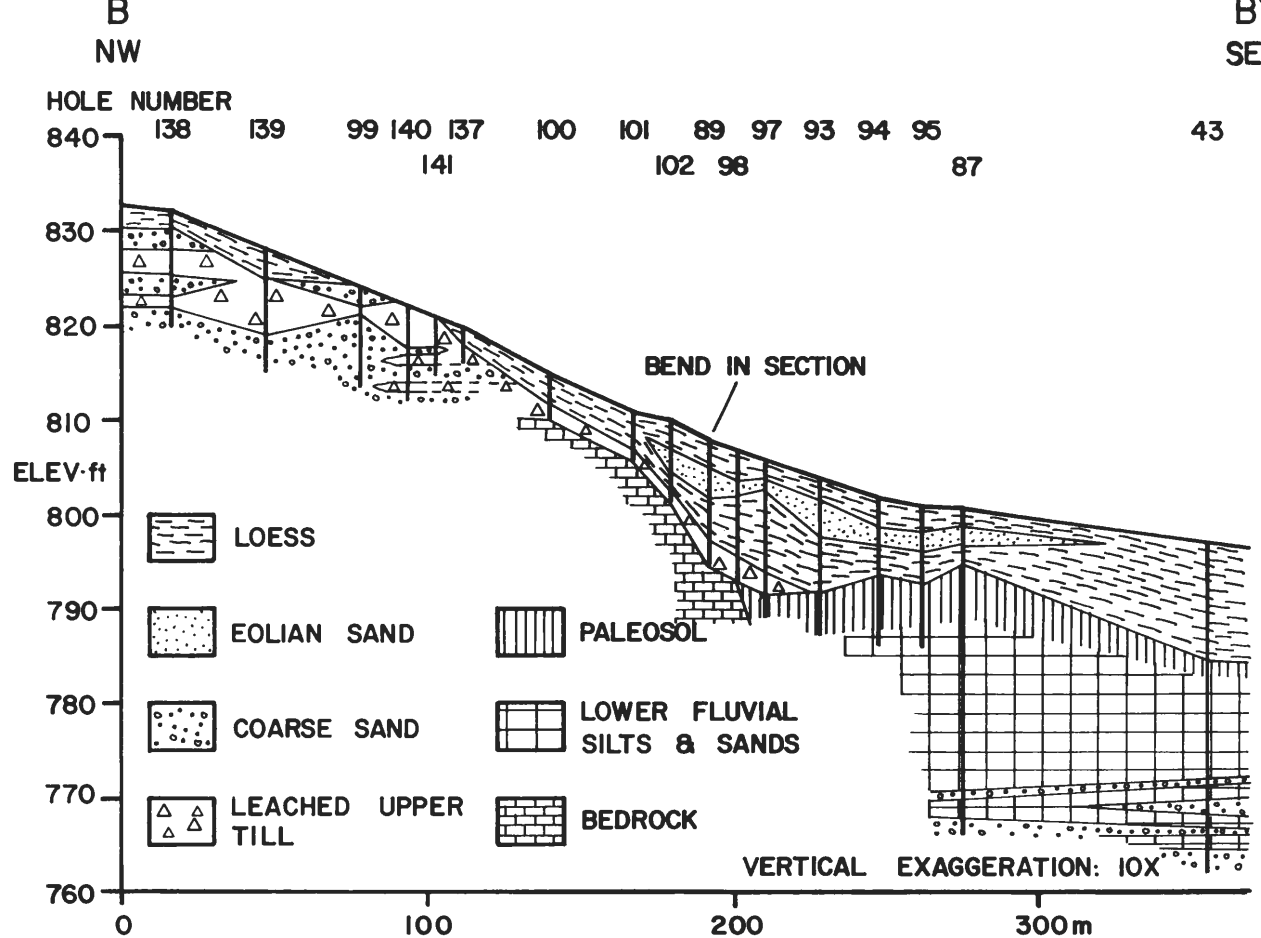


Figure 7. Cross-section along the axis of section 31 interfluvial (traverse B-B', Fig. 2).

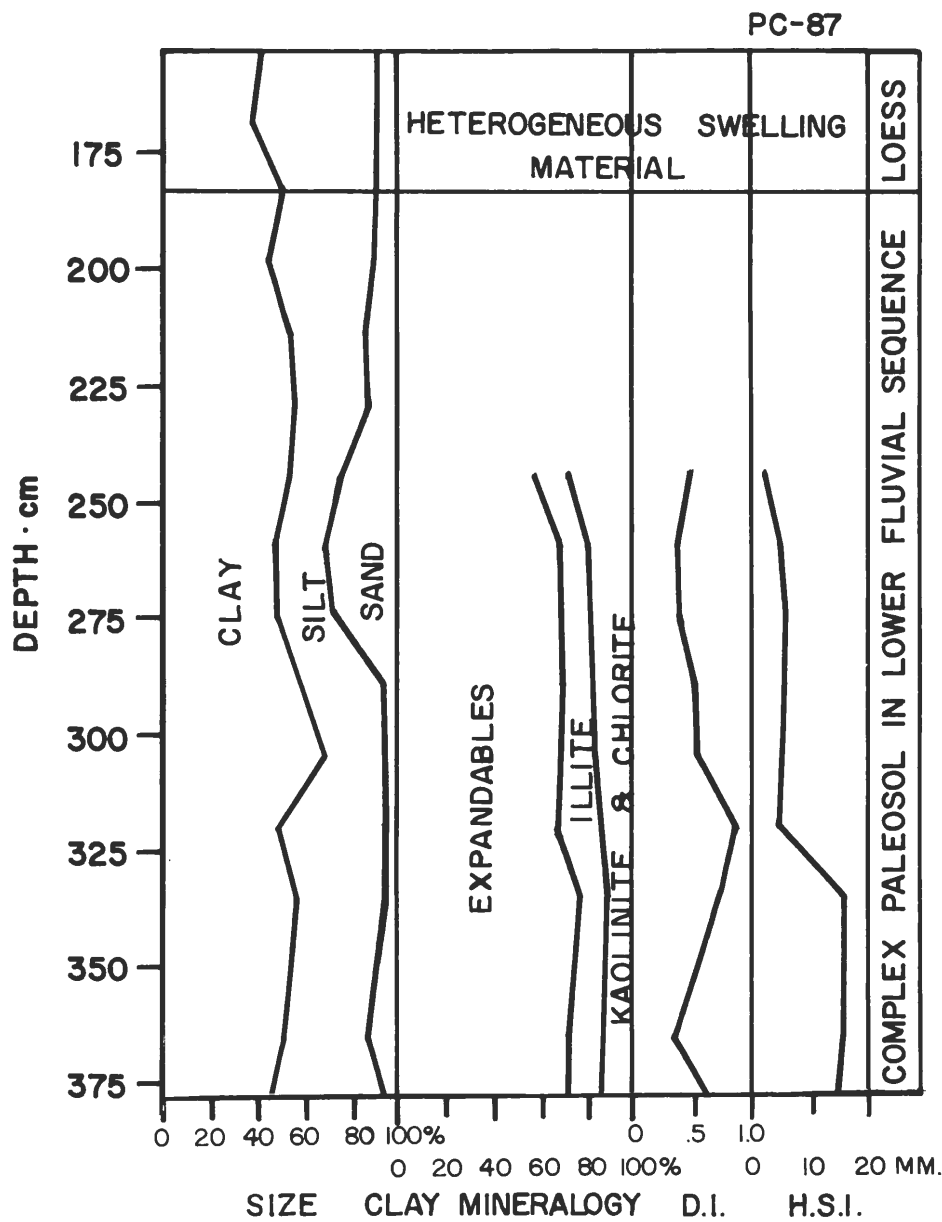


Figure 8. Laboratory analyses of the paleosol in hole 87 on traverse B-B' (Fig. 7).

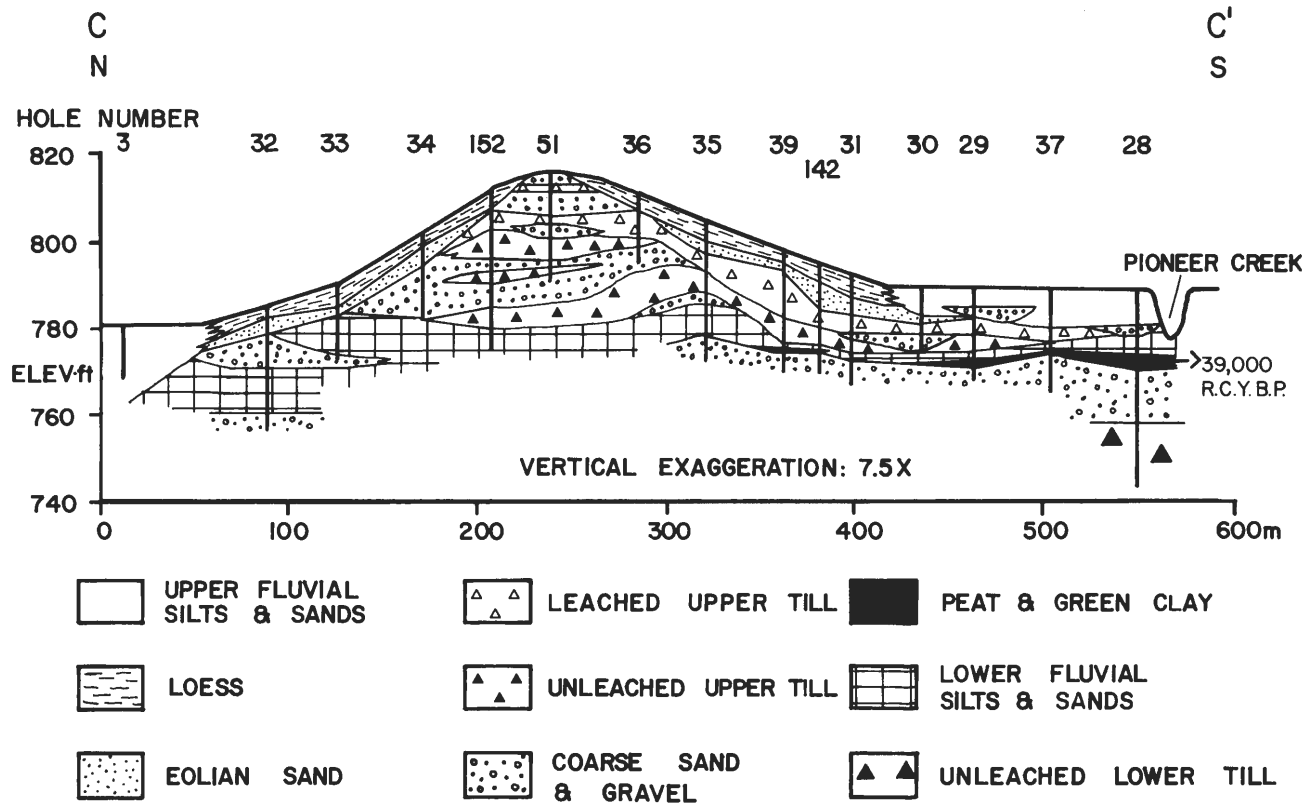


Figure 9. Cross-section through section 5 hill along traverse C-C' (Fig. 2).

this hill. Norton (1901) referred to this hill as a "short paha," but part of the stratigraphy is similar to that of the Iowan area. Secondly, this is the only place in the field area where there is firm evidence that two tills are present. Closely spaced boreholes and laboratory data show that an upper till must overlie a lower till (Fig. 9).

The thickness of the loess on this hill is characteristic of the loess in the Iowan area. Cultivation has induced erosion and probably has removed modern soil and loess from the hilltop. Loess is underlain by eolian sand which is traceable into the upper fluvial silts and sands of the flood plain of Pioneer Creek (Fig. 9).

The upper till, about 10.6 m thick, resembles that of both the Kansan and Iowan areas. It is similar to the upper till of the Stanwood paha in that it is leached in its upper 4.6 m under the crest of the hill (Fig. 9). The leached zone, however, is only 1.2 to 1.8 m thick on the southern flank of the hill (Fig. 9). A stone line separates the till from the overlying eolian sand, and paleosol is found in the till on the crest of the hill. These are characteristics of an Iowan area.

Figure 9 also illustrates how coarse sands and till may be interbedded in both the Kansan and Iowan areas. The upper till is underlain by coarse sands and gravels, and by the lower fluvial silts and sands (Fig. 9). Leached silt, green clay, and peat are found in holes 39 through 28 (Fig. 9). The peat was dated at greater than 39,000 R.C.Y.B.P. (I-4191) and is underlain by silts and coarse sands. The lower till is found at 9.1 m in hole 28.

CORRELATIONS

In the field area, there is evidence of at least two tills which are separated by a thick fluvial sequence. These tills may be two stades of a glaciation with the intervening fluvial sequence representing an interstade, or they may represent two glaciations of different age separated by deposits of an interglaciation. The latter view was accepted by earlier workers (Kay *et al.*, 1943). Classically the two tills would be considered to be Kansan and Nebraskan. However, because of stratigraphic "confusion" in the type areas of the Kansan and Nebraskan deposits (Hallberg and Boellstorff, 1978a), these two till units are now referred to as Pre-Illinoian in Iowa (Hallberg *et al.*, 1978b).

Pre-Illinoian

Few occurrences of a lower till in Cedar County are reported in the literature since the work of Norton (1901). Although the Quaternary deposits of the Stanwood paha are over 46 m thick, they are not described in the few existing well logs. The occurrence of the paleosol and leached fluvial silts and sands between the upper and lower tills are interpreted to indicate a period of weathering following deposition of the lower till. The stratigraphy and a pollen analysis (Szabo, 1975) of the peat in hole 28 indicate that it may have formed in an oxbow lake during a cool period before the next glaciation.

Here the upper till in the Iowan area is stratigraphically the same as the upper till in the Kansan area. Only one upper till appears to be present. The stratigraphy established from boreholes, the presence of a stone line in most holes in Iowan areas, and the presence of pedisediment support the work of Ruhe *et al.* (1968).

The upper till rests on sands and gravels or its lower part is interbedded with sands and gravels. In exposures where the upper part of this till has been eroded away, the interbedded sequence found in the lower part of the upper till may be better explained in two other ways: either the glacier incorporated older valley fill into its till, or it overrode its own outwash and incorporated this outwash into its till.

The Pre-Illinoian till deposits in Iowa are being assigned rock stratigraphic status (Hallberg *et al.*, 1978b). The upper till of the field area is a high-expandable, clay, mineralogy till, averaging 56% expandable clay minerals, 21% illite, and 23% kaolinite and

chlorite (Szabo, 1975). It correlates with the Wolf Creek Formation (Hallberg *et al.*, 1978b). Moreover, textural and mineralogical data (Szabo, 1975) indicate that it is likely to be the Hickory Hills Till Member of that formation. The lower till averages 39% expandable clay minerals, 26% illite, and 35% kaolinite and chlorite (Szabo, 1975) and correlates with the Alburnett Formation (Hallberg *et al.*, 1978b).

Illinoian through Early Wisconsinan

No major deposits in the field area may be definitely correlated to this time period, though possibly some of the coarse sands and gravels in Pioneer Creek valley were deposited during this time. The Yarmouth-Sangamon paleosol developed in the upper till shows the stability of the uplands in most of Iowa during this interval (Ruhe, 1969). No strong evidence of this paleosol is present in the study area, but it is found farther to the south in Cedar County (Miller, 1974).

Other paleosols developed during this time interval. The reddish-brown paleosol on the crest of the Stanwood Paha correlates with the Late Sangamon paleosol (Ruhe, 1956). The dark greenish-gray paleosol found in hole 79 of the Stanwood paha (Fig. 4) may be an erosional remnant of a Yarmouth-Sangamon accretion-ogley. But, the ease of penetration, its thickness (only .9 m), and landscape relations also suggest that it may be of Late Sangamonian age (G.R. Hallberg, oral communication). Pedogenesis also occurred in the exhumed accretion-ogley of section 31 interfluvium.

Late Wisconsinan

Radiocarbon dates (Miller, 1974) suggest that many deposits in the field area are of Late Wisconsinan age. The oldest deposit is the basal loess paleosol on the Stanwood Paha (Fig. 4). Miller dated a paleosol at the base of the loess on the Bennett Paha in east-central Cedar County at $25,100 \pm 700$ R.C.Y.B.P. (I-6750). He also dated an organic zone 2.4 m above this paleosol at $21,150 \pm 420$ R.C.Y.B.P. (I-7277). It is likely that the basal loess of the paha in the field area was deposited during this time.

The Iowan Erosion Surface was cut during Late Wisconsinan period. Miller (1974) dated its formation in east-central Cedar County between $17,810 \pm 280$ R.C.Y.B.P. (I-7295) and $21,150 \pm 420$ R.C.Y.B.P. (I-7277). Although the erosion surface could not be dated by radiocarbon in the field area, deposits similar to those reported in other studies (Ruhe, 1969; Miller, 1972) were found and are presumably of a similar age. Ruhe (1969) demonstrated that eolian sand on the Iowan surface may be traced into a sand zone intercalated in the loess of the paha. But near Pioneer Creek, the source of the eolian sand is valley deposits. The eolian sand in the loess in the section 31 interfluvium (Fig. 7) may be traced into sands of the valley. Likewise, the eolian sand in section 5 hill (Fig. 9) is traceable into valley deposits. Another source area for the sand zone of the loess is the fine sand under the upper till throughout the field area. If streams in the valleys had eroded through the upper till, the underlying sand unit would be exposed to wind erosion. The sand could be blown upslope and deposited with the loess.

Part of the upper fluvial silts and sands were also deposited during Late Wisconsinan. The peat in this fluvial sequence in the channel of Pioneer Creek in sec. 5, T. 82 N., R. 3 W. dated at $14,050 \pm 180$ R.C.Y.B.P. (I-7470). This correlates with Ruhe's (1969) average date of 14,000 R.C.Y.B.P. for the end of loess deposition. The interbedded silts and sands below this peat may be partly synchronous with the last increment of loess deposition in the field area. Wood from the upper fluvial sequence in N 1/2 sec. 5, T. 82 N., R. 3 W. dated at $13,560 \pm 320$, - 330 R.C.Y.B.P. (CWR-154). The flood plain of Pioneer Creek was apparently stabilized after 14,000 R.C.Y.B.P.

CONCLUSIONS

1. Near the classic Iowan-Kansan border in east-central Iowa, stratigraphic evidence indicates that two Pre-Illinoian tills are present.
2. Stratigraphically, the upper till in the Iowan and Kansan areas are the same till and correlate with the Hickory Hills Till Member of the Wolf Creek Formation.
3. The lower part of the upper till consists of interbedded till, sand, and gravel.
4. The lower till correlates with the Alburnett Formation.
5. Only a few deposits represent the time interval, Illinoian through Early Wisconsinan.
6. The eolian sand in the area is derived from Late Wisconsinan fluvial deposits, and/or from the Iowan erosion surface.

ACKNOWLEDGEMENTS

I wish to thank the University of Iowa and the members of the Department of Geology for support through a Teaching-Research Fellowship. I also wish to thank the Iowa Geological Survey for funding of radiocarbon dates.

LITERATURE CITED

- Alden, W.C., and M.M. Leighton. 1917. The Iowan drift. *Iowa Geol. Surv. Ann. Rept.* 26: 49-212.
- Calvin, S. 1896. Geology of Jones County. *Iowa Geol. Surv. Ann. Rept.* 5: 33-112.
- Chamberlin, T.C. 1895. The classification of American glacial deposits. *J. Geol.* 3: 270-277.
- Folk, R.L. 1965. Petrology of sedimentary rocks. Hemphill's, Austin. 159 p.
- Frye, J.C., H.D. Glass, and H.B. Willman. 1962. Stratigraphy and mineralogy of the Wisconsinan loesses of Illinois. *Illinois Geol. Surv. Circ.* 334. 55 p.
- Hallberg, G.R., and J.D. Boellstorff. 1978a. Stratigraphic "confusion" in the region of the type areas of Kansan and Nebraskan deposits. *Geol. Soc. Amer. Abs. with Programs* 10: 255.
- , T.E. Fenton, G.A. Miller, and A.J. Luttenegger. 1978b. Trip 2—The Iowan erosion surface: An old story, an important lesson, and some new wrinkles, p. 2: 1-94. *In: R.R. Anderson (ed.) 42nd Annual Tri-state Geological Field Conference Guidebook.* Iowa Geol. Surv. Iowa City.
- , J.R. Lucas, and C.M. Goodmen. 1978c. Semiquantitative analysis of clay mineralogy. *Iowa Geol. Surv. Tech. Inform. Ser. No. 8.* p. 5-22.
- , T.E. Fenton, and G.A. Miller. 1978d. Standard weathering zone terminology for the description of Quaternary sediments in Iowa. *Iowa Geol. Surv. Tech. Inform. Ser. No. 8.* p. 75-109.
- Iowa Geological Survey. 1917. [Map of Iowa showing drift sheets]. *Iowa Geol. Surv. Ann. Rept.* 26.
- , 1955. [Generalized sketch map of the glacial geology of Iowa]. *Iowa Geol. Surv.*
- Kay, G.F., E.T. Apfel, and J.B. Graham. 1943. The Pleistocene geology of Iowa. *Iowa Geol. Surv. Special Rept.* 262 p.
- McGee, W.J. 1891. The Pleistocene history of northeastern Iowa. *U.S. Geol. Surv.* 11th Ann. Rept. p. 189-577.
- Miller, G.A. 1974. Soil parent material stratigraphy and soil development, Cedar County, Iowa. Unpubl. Ph.D. dissertation, Iowa State Univ. 372 p.
- Norton, W.H. 1901. Geology of Cedar County. *Iowa Geol. Surv. Ann. Rept.* 11: 279-396.
- Ruhe, R.V. 1956. Geomorphic surfaces and the nature of soils. *Soil Sci.* 82: 441-445.
- , 1965. The Iowan problem. 16th Ann. Mtg. Midwest Friends of the Pleistocene Field Conf. Guidebook. 68 p.
- , W.P. Dietz, T.E. Fenton, and G.F. Hall. 1968. Iowan drift problem, north-

eastern Iowa. Iowa Geol. Surv. Rept. Inv. 7. 40 p.

----- . 1969. Quaternary landscapes in Iowa. Iowa State Univ. Press, Ames. 255 p.
Scholtes, W.H., and G.D. Smith. 1950. Some observations of the paha of northeast Iowa. Iowa Acad. Sci. Proc. 57: 283-291.

Soil Conservation Service. 1974. [Field maps of Cedar County, Iowa].

Szabo, J.P. 1975. The Quaternary history of the lower part of Pioneer Creek basin, Cedar and Jones Counties, Iowa. Unpubl. Ph.D. dissertation, Univ. of Iowa. 173 p.

Willman, H.B., H.D. Glass, and J.C. Frye. 1966. Mineralogy of glacial tills and their weathering profiles in Illinois: Part II, Weathering profiles. Illinois Geol. Surv. Circ. 400. 76 p.